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THE BIOLOGY OF THE RED SQUIRREL, *Tamiasciurus hudsonicus loquax* (Bangs), IN CENTRAL NEW YORK

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INTRODUCTION

The red squirrel is often a common and easily observed animal in parts of its range and has been the subject of a substantial volume of literature, yet many aspects of its biology remain unrecorded. This study concerns the southern red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs). Field work was done in central New York. The majority of observations and collections were made in Tompkins County in the vicinity of Ithaca. The study extended from October 1950 to July 1953; the most intensive field work was conducted from September 1951 through September 1952. Observations were made on all phases of the life history with particular

emphasis on pelage changes, reproduction, home range, territorial behavior, and age and growth characteristics.

Important previous studies devoted to this species are those of Klugh (1927), Hatt (1929), and Hamilton (1939). Hatt's study not only presents the results of his own investigations but also compiles much of the earlier literature pertaining to the red squirrel and related forms.

I wish to express my indebtedness to Professor W. J. Hamilton, Jr., under whose direction this study was conducted, for his valuable counsel, suggestions, and criticisms. Thanks are also due C. E. Parker and W. H. McKeon, New York State Con-

servation Department, for the many specimens they collected and the numerous other ways in which they aided me, and to the many other persons who furnished specimens or information. The photographs were taken by D. M. Payne. Acknowledgment is made to the following specialists who determined various nest associates and parasites of red squirrels: R. E. Crabill (centipedes), H. Dietrich and W. Stockton (Coleoptera), J. G. Franclemont (Lepidoptera), and B. V. Travis (intestinal protozoa), all of the Department of Entomology, Cornell University; G. F. Ferris (lice), Natural History Museum, Stanford University; W. J. Gertsch (spiders), American Museum of Natural History; C. C. Hoff (pseudoscorpions), Department of Biology, University of New Mexico; G. M. Kohls (ticks), Public Health Service, Rocky Mountain Laboratory, Hamilton, Montana; R. W. Strandtmann (mites), Department of Biology, Texas Technological College; and G. W. Wharton (chigger), Department of Zoology, University of Maryland. A final debt of gratitude is due my wife, whose encouragement and assistance have contributed in significant measure to the completion of this study.

This research was supported in part by a Graduate Student Honorarium awarded by the New York State Science Service.

MATERIALS AND METHODS

In addition to numerous hours of field observation, 575 squirrels were killed or live trapped during the study. Of these, 440 specimens for laboratory examination were obtained by shooting, steel and snap trapping, live trapping, and collection of road kills. The majority were shot, but rat traps baited with peanut butter or walnut meats were effective in taking animals during the winter, particularly in hedgerow habitats when tracks indicated areas of greatest activity. A few were collected with No. 0 steel traps which were set on the ground, lightly covered with leaves, and sprinkled with shelled corn. This method was little used since gray squirrels and chipmunks were taken equally often. Seven live trapped animals were killed to obtain undamaged skeletons, fresh reproductive tracts, or to check for intestinal protozoa.

Specimens were weighed and searched for ectoparasites as soon after collecting as possible. Total, tail, and hind foot lengths were recorded. Conventional or flat skins were prepared, or notes on pelage characteristics and molt pattern taken. The condition of the serotum; appearance of the testes, seminal vesicles, prostate, and bulbar region; size of cauda epididymal tubules; and presence or absence of sperm in the epididymis were noted for males. Measurements were made of the length of the penis, seminal vesicles, and prostate; and the length, width, and weights of testes were recorded. A series of seminal vesicles and prostates were preserved in 10% formalin for subsequent volumetric determinations. Females were examined for condition and size of nip-

ples; incidence of lactation; and condition of the reproductive tract, i.e., virgin, anestrus adult, semi-turgid, fully turgid (estrus), early pregnancy, advanced pregnancy, recent partus, or post partus. The presence or absence of follicles and corpora lutea and relative development of these structures, if present, were reported, and the number of uterine swellings, embryos, or placental sites were noted. Measurements were taken of uterine and vaginal width, and size of the ovaries. Most of the female genital tracts were preserved for later study. Reproductive tracts of males and females showing representative stages of the reproductive cycle were fixed in 10% formalin or Bouin's solution for subsequent histological preparation.

Stomach contents were weighed and recorded with time of death if known and the contents analyzed for frequency of occurrence of general food types such as mast, fungus, fleshy fruits, etc.

Skulls, scapulas, pelvic girdles, humeri, and femurs were collected and cleaned by dermestid beetles for studies of individual, secondary sexual, and age variation. A series of weights of body organs of adults, and measurements of anal glands of males and females at different seasons were also secured.

Live trapping studies were conducted with the No. 2 size (24 in. x 7 in. x 7 in.) "Havahart" animal trap manufactured by the Allcock Mfg. Co., Ossining, New York. The number of traps employed varied from 5 to 17. Shelled whole corn proved to be the most satisfactory bait. Seven species of mammals and 12 species of birds were captured incidental to red squirrel trapping operations.

One hundred and forty-nine red squirrels were live trapped. Seven were killed to obtain skeletons or other data, 22 were kept in captivity for periods ranging from 2 days to 10 months, 1 died in the trap, and 3 succumbed during handling. Of the 116 squirrels marked and released, 59 were never retaken, while the remainder were retrapped a total of 180 times. The average number of recaptures per individual was 3.1; one squirrel was retrapped 15 times. In addition, several hundred sight observations were made on marked animals in the field.

There appeared to be no variation in trapability between individuals or sexes, nor any obvious tendency to avoid traps after repeated captures. Similar observations were made by Linduska (1950). Field observations indicate that squirrels find the traps by random foraging on the ground and are probably not attracted to the bait from more than 10 or 15 ft. away. However, once the location of the trap and its food source is learned the animals will often return regularly and be recaptured if the trap is left in the same location. This behavior is an important consideration in home range and population studies based on live trapping data. There is good indication of a seasonal variation in the susceptibility to trapping in some habitats that can be explained by the feeding habits of the squirrels at these times. Linduska (1950) noted a yearly fluctuation in the susceptibility to trapping.

tuation in trapability that was correlated with a shortage of natural foods.

Since most red squirrels are extremely nervous when captured and struggle violently to escape, the traps were checked at least twice daily at about 8 or 9 a.m. and again about dusk. Usually they were also visited about noon, and during very cold weather even more frequently. The most convenient way of handling trapped animals was to run them into a flour sack where they could be weighed, examined, and marked. The sacks were reweighed each time used since they would vary several grams with the accumulation of dirt, urine, etc. Examination and marking were accomplished by grasping the squirrel about the shoulders while in the bag and then folding back the sack to expose the rear part of the body. The animals will remain relatively quiet if the eyes are kept covered. Anesthesia was occasionally employed and resulted in the death of one individual. Only one red squirrel was lost by "shock" while being handled; it seems that this species is much less subject to this affliction than fox squirrels (Allen 1943) and gray squirrels. The site and approximate time of capture, weight, pelage condition, appearance of external genitalia, abnormalities, parasites, and other data were recorded for trapped animals on individual record sheets.

Squirrels were marked for permanent recognition by incising toes with sharp scissors according to a

scheme in which the toes of the fore feet are numbered from one to eight and those of the hind feet from 10 to 100 (Fig. 1A). With this combination it is possible to mark 143 individuals consecutively (numbers with the figure "9" cannot be used) without removing more than a total of three toes and never more than a single one from a foot. Since claws or entire terminal phalanges are occasionally lost under natural conditions it is desirable to remove at least half of the digit when marking. Loss of toes does not in any observable way hinder normal activity of the squirrels, and the severed digits heal in a few days. The animals were marked for visual recognition in the field by a system of removing fur from certain numbered areas of the body (Fig. 1B). It was found more expedient to refer to such a fur clipped animal as "number 14" rather than by the actual identifying marks as "left shoulder-right side of base of tail." By using only one or two marks it was possible to number 49 individuals consecutively and 38 more with additional combinations. No serious disadvantage was experienced from the necessity of placing marks on different sides of the body. Shearing the distal colored portion of the hairs from an area the size of a 25 cent coin exposes the blackish basal part of the fur and leaves a dark patch that can be discerned with 7 x 50 binoculars at 400 ft. Fur clips persist until the next molt. After a molt period has passed the same marks can be used again.

WEIGHTS AND MEASUREMENTS OF ADULTS

External Measurements. Means, standard errors of the mean, and extremes of total, tail, body, and hind foot lengths of 256 adult males and females are given in Table 1. All measurements were taken from freshly killed specimens. Total length, tail, and hind foot were measured in the conventional manner. Tail length was subtracted from total length to obtain body length. Although the differences are small, females average larger in all dimensions except hind foot. Tail length is the most variable of the external measurements, even though specimens with injured tails were not included in the sample. Body length is next, while hind foot and total length exhibit the least variation.

Body Weights. Table 2 summarizes the body weights of 285 adults by months. Males average slightly heavier than females, and their degree of variability in this respect is somewhat less. Although perhaps not statistically significant, slight seasonal variation in mean weights of both sexes is suggested. Weights vary somewhat between habitats but, because of the different times of the year in which samples were collected, cannot be critically compared. Climax forest types (beech, hard maple, and hemlock) produced adults with the highest average weight (198.55 gms), but it is probable that habitat suitability as reflected in biomass is more a function of local conditions rather than an overall effect of a particular association.

Organ Weights. Weights in milligrams of the heart, lungs, liver, spleen, kidneys, and adrenals

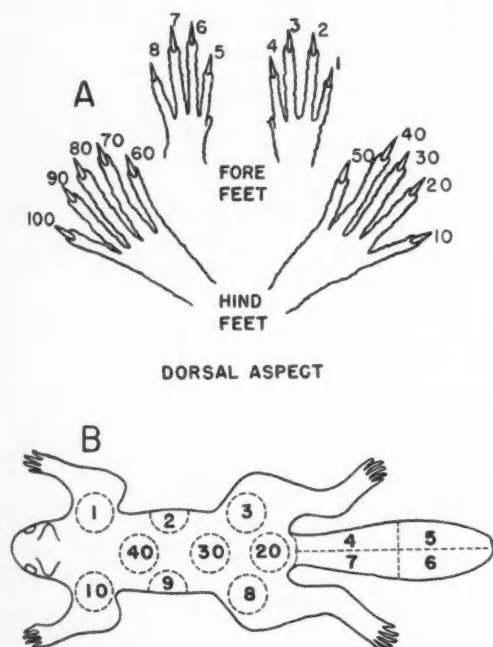


FIG. 1. Methods of marking squirrels in live trapping studies. A. Number scheme used in marking for permanent recognition by a series of toe clips. B. Method of numbering used in marking animals by fur clipping for field recognition.

TABLE 1. External measurements in millimeters of 149 adult male and 107 adult female red squirrels from central New York.

Measurement	MALES		FEMALES		TOTAL	
	Mean and SE	Range	Mean and SE	Range	Mean and SE	Range
Total Length.....	310.1±.94	282-333	310.2±1.16	282-336	310.2±.73	282-336
Tail Length.....	123.7±.63	106-142	125.0±.85	105-145	124.3±.56	105-145
Body Length.....	184.7±.66	165-206	185.2±.70	167-202	185.0±.46	165-206
Hind Foot.....	48.2±.14	44-52	47.6±.15	44-51	48.0±.10	44-52

from 18 freshly killed adult males and 12 adult females are compared with those of corresponding organs of white rats of comparable body weight (Table 3.) Data for the rats is from Donaldson (1924). In both species the average organ weights of the males exceed those of females, except for the liver and spleen in squirrels and the adrenals in the rat. The liver, spleen, and kidneys of rats are heavier than in the red squirrel, whereas the heart, lungs, and adrenals are considerably lighter. This is what might be suspected in comparing a highly active animal with a less active one.

Skeletal Variations. The means, standard errors of the mean, and ranges of ten linear measurements of skulls and other skeletal parts have been recorded

TABLE 2. Average monthly weights in grams of 186 adult male and 99 nonpregnant adult female red squirrels from central New York.

Month	MALES			FEMALES		
	Number	Mean	Range	Number	Mean	Range
January....	15	194.99	167.1-220.0	7	192.60	176.2-211.8
February....	26	161.72	128.9-226.1	16	184.77	127.3-224.1
March.....	26	188.96	157.9-225.3	8	188.06	166.5-203.5
April.....	20	192.90	168.8-229.3	10	172.57	158.7-208.3
May.....	16	201.07	189.7-246.7	7	194.41	171.4-242.8
June.....	18	199.53	172.9-224.4	16	205.89	171.7-241.5
July.....	18	193.17	169.3-226.6	2	180.50	172.1-188.0
August.....	12	197.17	172.9-226.0	7	197.67	181.7-226.5
September..	13	183.05	153.9-216.1	14	182.98	157.4-206.5
October.....	2	188.30	180.2-196.4	9	181.88	155.3-203.1
November..	9	195.05	174.4-214.5	2	196.75	185.0-208.5
December..	11	198.63	182.5-243.2	1	174.7
Total.....	186	193.70±1.30	128.9-246.7	99	188.80±1.94	127.3-242.8

TABLE 3. Weights in milligrams of organs of adult red squirrels and white rats of comparable body weight (males 194.1 gms, females 188.5 gms). Data for rats from Donaldson (1924).

Organ	<i>Tamiasciurus</i>				<i>Rattus</i>	
	MALES		FEMALES		MALES	FEMALES
	Mean	Range	Mean	Range	Mean	Mean
Heart.....	1,632	1,220-2,170	1,539	1,070-2,000	782	765
Lungs.....	2,615	1,820-3,450	2,446	1,750-4,950	1,147	1,119
Liver.....	5,944	4,450-8,750	6,540	4,770-9,090	9,820	9,600
Spleen.....	447	220-1,000	496	300-1,270	519	505
Kidneys.....	1,389	1,090-1,840	1,374	1,050-1,790	1,664	1,622
Adrenals.....	91	50-100	87	70-100	34	50

(Table 4). Four skull measurements taken were: length of skull from the posterior end of the cranium to the tip of the nasal bones, greatest breadth across the zygomatic arches, length of the cheek tooth row, and length of the mandible from the condyle to the tip of the incisor. Scapular length was taken from the lower edge of the glenoid cavity to the caudal extremity of the glenovertebral angle and the width as the greatest distance between the glenovertebral and coracovertebral angles. The length of the pelvic girdle was measured from the posterior point of the superior ischial tuberosity to the most cranial extremity of the ilium. The distance between the two femoral processes, anterior to the acetabulum, was denoted as pelvic width. Humeral length was measured between the head and trochlea, and that of the femur between the greater trochanter and the lateral epicondyle. Vernier calipers were used to obtain measurements to .1 mm.

Males slightly exceed females in all dimensions except the zygomatic breadth, cheek tooth row, and length and width of pelvic girdle, but the differences are only average ones and too minor to be of any value in separating sexes. Excepting the cheek tooth row, skull measurements have the lowest coefficients of variation of any measurements taken (Table 5). The frequency of occurrence of the minute first upper premolar is not significantly different in the two sexes. This tiny peg tooth was visible in 67.7% of 118 male skulls and in 70.3% of 91 female skulls.

TABLE 4. Measurements in millimeters of skeletal structures of adult red squirrels from central New York.

Measurement	MALES			FEMALES		
	No.	Mean and SE	Range	No.	Mean and SE	Range
Skull.....	50	50
Length.....	..	45.64±.13	43.8-47.2	..	45.47±.14	43.7-47.2
Zygomatic Breadth.....	..	26.48±.08	25.3-27.7	..	26.56±.09	25.3-27.8
Cheek Tooth Row.....	..	7.20±.05	6.7-8.0	..	7.32±.08	6.3-8.1
Mandible Length.....	..	31.15±.10	29.7-32.5	..	31.00±.09	29.7-32.5
Scapula.....	84	73
Length.....	..	22.22±.07	20.5-23.9	..	21.73±.08	19.9-23.1
Width.....	..	16.94±.08	14.9-19.3	..	16.51±.08	15.0-18.5
Pelvic Girdle.....	72	50
Length.....	..	32.93±.12	30.9-37.3	..	33.38±.16	31.4-35.8
Width.....	..	17.58±.37	16.2-19.1	..	17.83±.08	16.4-19.3
Humerus.....	106	31.65±.08	29.8-34.0	83	31.29±.95	29.3-33.4
Femur.....	74	39.18±.13	37.0-42.2	56	38.85±.15	36.0-42.1

TABLE 5. Coefficients of variation (CV) of 15 measurements made on adult red squirrels.

Measurement	MALES		FEMALES	
	Number	CV	Number	CV
External.....	149	107
Total Length.....	..	3.20	..	3.62
Tail Length.....	..	5.37	..	6.62
Body Length.....	..	4.34	..	3.89
Hind Foot.....	..	3.55	..	3.36
Body Weight.....	186	9.16	99	10.22
Skeletal Structures				
Skull Length.....	50	2.03	50	2.20
Zygomatic Width.....	50	2.38	50	2.41
Cheek Tooth Row.....	50	5.00	50	8.61
Mandible Length.....	50	2.22	50	2.26
Scapular Length.....	84	3.28	73	3.36
Scapular Width.....	84	4.49	73	3.69
Pelvic Length.....	72	3.19	50	3.35
Pelvic Width.....	72	3.36	50	3.25
Humeral Length.....	106	2.62	83	3.04
Femoral Length.....	74	2.81	56	2.90

Bangs (1896) stated that this tooth was absent in more than half of *Tamiasciurus h. hudsonicus* examined.

The only morphological sexual difference apparent in the skeleton is in the relative development of the inferior ischia tuberosities (Bryant 1945), corresponding to the areas required for attachment of the crura of the penis and clitoris. Using this character, the sexes of adults can be established at a glance, since the tuberosities are massive in the males and only small tubercles in the females. Young animals cannot be sexed in this way as the full development of the tuberosities in males does not occur until the approach of sexual maturity.

Variability of Measurements. Coefficients of Variation for the 15 measurements taken are given for each sex in Table 5. The values for the females slightly exceed those of the males in 11 of the 15 measurements, suggesting that the former are somewhat more variable in most of their dimensions. This contrasts to the general supposition (Schultz 1926) that the males of birds and mammals tend to exhibit the greater variability.

PELAGE CONDITION

Adult Variation. Winter and summer pelages exhibit a certain degree of individual variation that is apparently not correlated with sex or age. The middorsal band is the most variable feature of the winter pelage. It ranges from a bright, well defined rufous stripe in which the aristate guard hairs have only a narrow black tip to an indistinct dark reddish-brown band in which most of the guard hairs have a broad subterminal black ring besides the proximal plumbeous portion and black tip. The bright, clear middorsum phase is uncommon. An intermediate type with a fairly bright stripe but with a larger proportion of ringed guard hairs, particularly between the shoulders and on the upper back, is more frequent; while the dark, heavily black-banded dorsal stripe

is encountered in the majority of specimens. The ratio of black-banded, intermediate, and clear middorsal phases in 155 specimens collected from December to March was 8 : 2 : 1.

The lateral stripes are generally faintly indicated as a dusky area between the dorsal and ventral coloration. In some individuals they are completely absent and in others quite distinct. Their relative intensity is due to the proportion of guard hairs present that have a longer black tip than those typical of the lower sides. Allen (1890) concluded that the presence of dusky side stripes and a poorly developed middorsal band in winter were indications of immaturity. Although these features may occur together, they have no apparent relation to age, since subadults from fall litters frequently attain a brighter winter coat with less distinct lateral stripes than many old adults.

The color of the sides is occasionally an ashy gray, but usually is more olivaceous. Frequently, a yellowish suffusion borders the middorsal band or is noted in the shoulder region. Ear tufts are invariably present when the molt is complete but vary in length and density of furring. They may be either reddish or blackish in color. The long ventral fur is usually vermiculated with black only in the area of the knees, but in some individuals the underparts are also lightly vermiculated along the mid-ventral region. Occasionally, the entire venter is heavily marked in this way.

In summer the color of the fore and hind feet, fore limbs, and shoulders varies from a light yellowish-gray to a deep orange-cinnamon shade. The color of the rest of the upper parts is generally a glossy olive-brown vermiculated with black and is darker and richer in hue along the middorsum. Infrequently, the sides are grayish. A more common variation is that in which the entire dorsum has a reddish cast. Such individuals also tend to have a more intense coloration of the fore limbs, shoulders, and hind feet. According to Allen (1898) the olivaceous and rufous color phases occur in the ratio of about 4 to 3 throughout the *Tamiasciurus hudsonicus* group.

The lateral stripes vary from a thin sharp line to a wide black band and are infrequently interrupted on one side. Rarely, a specimen is noted with the stripes brown instead of black.

Juvenile Pelage. The juvenile coat has not been adequately described. Allen (1898) states that the first coat of the young is similar to the summer coat of adults. Hatt (1929) noted that young in the southern Adirondacks were a brilliant rufous on the back and flanks while adults were more olivaceous; and Goodwin (1935) indicates immature specimens are darker and duller than adults.

The juvenile pelage is soft and long, closely resembling the texture of the adult winter coat. The ears usually bear prominent tufts, and the bottoms of the feet and digits are thickly furred except for the plantar tubercles. The pelage exhibits three

general color phases, gray, olivaceous, and reddish, although intermediate types are not uncommon. The typical gray phase is markedly similar in color to the adult winter pelage. The middorsal band is prominent (but always black banded), the sides, limbs, and feet are grayish, and the lateral stripes obsolescent. Juveniles of the olivaceous phase resemble summer adults in coat color but not texture. The fore limbs and hind feet are yellowish-orange, and the upper parts olive-brown, with the middorsal region often slightly reddish. The side stripes are distinct and black, but are not usually as trenchant as in adults. Typical specimens of the reddish type have the middorsum a clear, deep reddish color which extends down the sides to the lateral stripes. In some, the guard hairs are entirely red, lacking the usual plumbeous basal portion. The fore limbs, shoulders, and hind feet of these erythristic individuals are usually a rich orange-red. Of 17 juveniles live trapped on one study area in June and July, 8 were of the gray phase, 7 were reddish, and 2 were olivaceous. Young belonging to the same litter apparently have similar pelage coloration.

Mearns' (1898) statement that young born early in the season are clothed in winter pelage is probably based on observations of young of the typical gray phase. I found no correlation between the winter type pelage and time of birth. Individuals of approximately equal age and representing all three color variations were collected during the same period in early summer. While the series is smaller, no typical winter-type juveniles were handled or observed in the fall. There is the possibility that the type of pelage or molt stage of the mother during the gestation period influences the pelage coloration of the young, rather than the actual time of birth.

Aberrations. Abnormal color variants are uncommon in the red squirrel. Albinos, some of which may be extreme cases of white spotting, a genetically distinct phenomenon, have been reported by Penant (1792), Mearns (1898), Miller (1899), MacFarlane (1905), Seton (1909), Dunn (1921), Wood (1922), and Engles (1933). Specimens recorded as "partially albinistic" are probably cases of white spotting. Such individuals with white areas variously developed on the body and tail are noted by DeKay (1842), Bangs (1896), Wood (1922), Dice (1925), and Klugh (1927). Examples in which the white is restricted to the tail, usually the distal portion, are cited by Bell (1898), McElhinney (1923), and Seton (1929). Melanic specimens are rare. Allen (1898) notes an intensely black specimen collected at Nulato, Alaska, while Adams (1873) indicates that an entire melanistic population of red squirrels existed on the south coast of New Brunswick.

Among the large number collected or observed in central New York, four squirrels showed slight white spotting. One male had the left hind foot and the toes of the right hind foot pure white. The claws also lacked pigment. A male and female had small patches of white hairs on the back and upper lumbar

region, and another male possessed a tuft of white hairs intermixed with the normal hairs on the tip of the tail. This latter condition may have been caused by an injury to the tail. There is a specimen in the Cornell University Collections taken in the western portion of the state that is very white on the upper parts of the body, although the guard hairs are plumbeous at the base and many retain a slight pigmentation. The hair on the ears is normally colored, and the fur on the rump and the lower parts of the fore and hind limbs and feet is darker and more typical in color. The tail is normal. W. J. Hamilton, Jr. (personal communication) has also observed such a predominantly white specimen at Ithaca.

Another individual (C. U. 4618) collected in Tompkins County is in strikingly aberrant winter pelage. The middorsum is a vivid rufous which shades into ochraceous-orange on the upper sides and ochraceous-buff on the lower sides and external surfaces of the limbs and feet. The pelage is vermiculated with black only on the forehead and rostrum. Preble (1908) records a somewhat similarly colored animal from the Mackenzie-Athabaska region of Canada.

A juvenile female killed June 15, 1953 had large gray patches on the middle of the back and on the right hind leg. The pelage was normal on the remainder of the body. The coloration was apparently due more to the lack of guard hairs and the prominence of the grayish underfur in the abnormal areas than to actual depigmentation of the individual hairs. A specimen studied by Svihla (1931) had large gray patches that were due to an actual loss of pigment in many of the hairs.

Seasonal Changes. Detailed data on molts have been obtained from records of pelage condition and molt of all squirrels live trapped or autopsied, a selected series of 148 flat skins showing all stages of the yearly pelage cycle, observations on 20 animals kept in captivity during the molt periods, and numerous field observations. Other studies (Allen 1890, Hatt 1929, and Hamilton 1939) have indicated two annual body molts for this species but have failed to state that the tail is molted only once during the year. A molt undergone by spring juveniles in mid-summer has apparently not been previously recognized. Since these animals also molt in the fall and following spring, they may actually complete three molts in slightly over a year. The pattern of the spring molt in central New York (Fig. 2) is essentially similar to that described by Nelson (1945) for *Tamiasciurus h. hudsonicus* in Minnesota. New fur appears first on the digits or upper part of the hands or on the top and sides of the snout, although it may appear almost simultaneously in both regions. About the same time, or slightly later, summer hairs become visible on the hind feet. Frequently they first appear on the distal phalanges or on the inner half of the foot from whence they spread over the entire foot to the ankle. The main progression of the molt is now in a caudal direction. The pelage of the

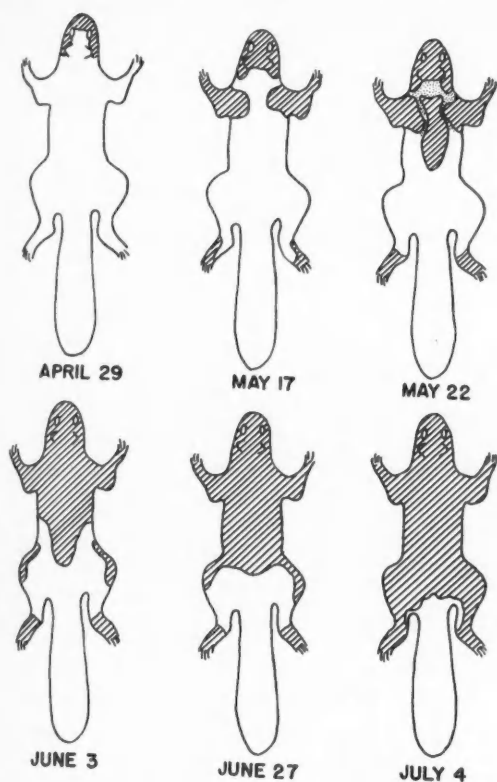


FIG. 2. Stages in the spring molt of a captive adult female. Shaded areas indicate fresh summer pelage. Stippled area denotes intermixture of old and new pelage.

head is replaced on the crown and beneath the eyes to the base of the ears, while summer fur extends up the fore limbs, often first on the anterior or posterior edge, onto the shoulders. Occasionally new fur appears on the shoulders before the upper arms evidence any change. Upon coalescence of the molted areas of the head and shoulders, a patch of winter hair may be isolated on the crown or nape. It grows smaller but often persists until the molt is nearly complete. In the majority of specimens a strip of summer fur has developed on the anterior edge of the hind legs from the groin to the knee by the time the shoulders attain summer pelage. The molt proceeds posteriorly on the middorsal region and upper sides, a ragged appearing intermixture of winter and summer fur often bordering the completely molted portions. As the replacement of fur extends to the lower sides, the lateral stripes become visible, with the middle part often the last to become fully intense. The rear edge of the hind legs and the rump just above the base of the tail are the last to attain fresh pelage. By the time the summer coat is complete, the ear tufts, which begin to show thinning when the molt reaches the shoulders and

anterior part of the back, have usually been lost.

The long grayish winter fur on the venter is replaced by the short white pelage of summer coincident with the change of the upper parts. Progressing in the same direction as the dorsal molt, fresh pelage covers the lips and chin, then appears on the throat, upper breast, and inner portions of the fore arms. It usually extends caudally along the midline before spreading laterally. In some lactating females new fur is present medial and lateral to the nipple line before the old fur surrounding the teats is lost. The inguinal region and posterior parts of the hind limbs are the last to be molted.

The progress of the molt is gradual and is seldom marked by a distinct molt line. Usually there is a fairly sharp demarcation between the summer and winter pelage, but in some cases the change is very diffuse, giving the dorsum a blotched aspect of small patches of summer fur intermingled with areas of winter pelage and intermixture of both types. Judging from the percentage of specimens taken at different stages of the molt and from observations on captives, the fur on the feet and head is attained in a short time, then follows a period in which little visible change occurs, after which the pelage over most of the dorsum is replaced rather rapidly. Traces of winter fur on the rump and hind legs then persist for some time before the molt is finally fully completed.

The period of the spring molt extends from late March to early July. Adults collected March 26, 27, and 30 had summer hairs on the fore and hind feet and the skin unprime between the eyes and ears and on the snout. By April 15, about 90% were molting, and of these, 70% had new fur only on the forehead, feet, or limbs and 30% showed the molt advanced over the anterior half of the body. During the last half of the month, 60% had summer fur on the anterior half of the body and only 40% had it limited to the feet or forehead. All adults were molting or had finished by the middle of May. Over half of the molting individuals had new fur on the anterior or posterior regions of the body, and about 6% had already completed the molt. The first specimen with the molt complete was noted on May 4. One third of the specimens collected or observed during the period May 15 to 31 were in full summer dress, and new pelage had reached the rear parts of the body of about three fourths of those specimens still molting. Nearly 70% had the summer coat by the middle of June and no wild adults were observed molting after the first week in July.

During the latter part of the molting period, comparisons of adult males and females collected or observed over the same time interval showed the males to average slightly more advanced in the molt, although both sexes seemed to begin changing at approximately the same time. The somewhat retarded rate of molting in the females cannot be clearly related to the incidence of lactation, since as often as not lactating or recent partum females were as

advanced in the molt as the average male at that time. Somewhat scanty data also suggest that some subadult females (males mature before the inception of the spring molt) may begin molting at a later date than adults.

Wild squirrels probably complete the molt in less than two months. The change may progress quite rapidly in some individuals. One live-trapped adult male had molted only the head, fore limbs, and shoulders on April 5 and when retaken 24 days later only a strip of winter fur on the rear edge of the hind legs and rump remained. A recently lactating female had new fur only on the face, feet, and between the shoulders on June 22 but had completed the molt by July 1. Captive animals often do not begin the molt as early as wild ones and may take considerably longer to accomplish the change, perhaps as a result of the physiological or psychological effects of confinement. Seven animals confined in large outdoor cages completed the molt in periods ranging from about 54 to 137 days, with an average of approximately 81 days. Exact dates of onset and completion of molts were not available as the captives were usually checked for molt only at weekly intervals. A captive studied by Nelson (1945) required between 120 and 135 days to complete the molt.

The hairs on the tail are apparently replaced only once annually as in the gray squirrel, *Sciurus carolinensis* (Roegner 1950, Morrison-Scott & Bishop 1952). The fall molt (Fig. 3) commences with that of the tail. The change of the hairs is gradual and its progress difficult to follow unless fur is clipped off various parts of the tail and the sequence in which it is replaced noted. New hairs generally seem to appear first at the base and then distally. They are usually more orangish than the old hairs, and the freshly molted tail is noticeably brighter, more lustrous, and denser than the dull, worn tail of the summer pelage.

The course of the body phase of the fall molt is the reverse of that of the spring. New fur appears initially on the rump just above the tail, spreads to the rear portions of the hind legs and begins to move cephalad over the body. It may sweep generally over the entire dorsum and down onto the lower sides, or extend as narrow bands at about the middle of each side of the body before spreading dorsally and ventrally. Often a patch of winter fur develops on the nape or between the shoulders while the main molted area has progressed only to the lumbar region and the intervening region shows no replacement. Typical winter pelage soon covers the dorsal parts of the body to the shoulders, ankles, and posterior edge of the ears. The last areas to become clothed are the fore limbs, hind feet, and a strip on the anterior edge of the hind legs extending from the knee to the groin. The summer fur persists longest on the feet and digits, the replacement on the hind feet usually beginning first on the outer half of the foot. The ear tufts may begin to grow during the final phase of the body molt but do not

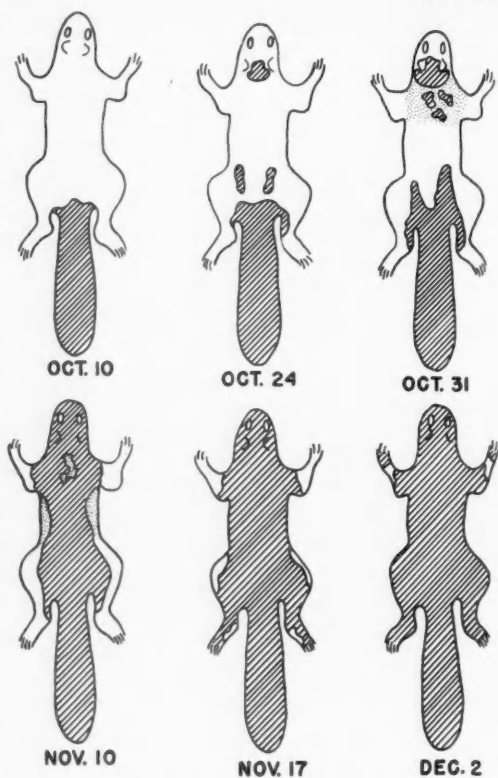


FIG. 3. Stages in the fall molt of a captive adult male. Shaded areas indicate fresh winter pelage. Stippled areas denote intermixture of old and new pelage.

become fully prominent until the winter coat is complete. The change on the venter generally proceeds forward from the inguinal region but occasionally the entire underparts show incipient molt and gradually attain the long winter fur throughout. There is no increase in the intensity of coloration of either the summer or winter coat after the completion of the molt as implied by Hatt (1929) and Hamilton (1939).

The fall molt is in progress from late August until early December. Tail molt was beginning on adults collected August 17 and 18 and had been completed on specimens taken September 13 and 14. The majority of adults probably molt the tail in early September. The earliest date on which body molt was observed was September 22, and about 5% of the adults were molting during the latter half of the month. New pelage had not progressed beyond the posterior parts of the body. During the same period in October over 90% were molting, and in over half of these the replacement of fur had advanced to the anterior parts of the body. In November all adults were molting on the shoulders and head, and the first individual in complete winter pelage was collected November 18. All squirrels had completed the molt by December 7.

No differences between adult males and females in the rate of molting can be ascertained in the fall. Spring juveniles apparently commence the molt at about the same time as the adults, but most summer juveniles are not in full molt until almost a month later. Two juveniles approximately 12 weeks old when captured on November 2 did not exhibit any pelage changes until November 22. Three captive adults who attained winter pelage in approximately 45, 50, and 60 days, respectively, offer slight evidence that the fall molt, excluding the tail, is accomplished in a shorter time than that of the spring.

Spring juveniles when about 12 to 15 weeks of age undergo a molt in which their soft, fuzzy coat is replaced by pelage typical of the summer adults. A similar molt is noted for the gray squirrel by Shorten (1951). Fewer observations were made on young born in the latter part of the summer and early fall but they apparently do not have this extra molt, changing directly to the typical adult winter coat. The order of the juvenile molt is similar to that of the adult spring molt. Dorsally, the new fur spreads from the fore feet or head caudally over the back and sides. The hind feet change shortly after the molt is initiated. Fresh pelage on the venter is first visible on the chin and breast and moves posteriorly to the inguinal region. By the end of the molt the ear tufts are reduced to a few hairs or are lacking, and the furring on the soles of the feet is largely gone. Unlike the spring molt of adults, the tail is also molted at this time. There is no tail molt preceding the regular fall molt in spring juveniles.

The juvenile molt occurs in the majority of the young from late June to early September. The earliest molting juvenile, which had new hair visible beneath the old fur on the fore arms, was recorded June 24. About 90% were molting in July, and the first with a complete new coat was noted July 30. By the middle of August, over half had completed the molt and by the end of the month most were in full summer pelage. Individuals of approximately the same age may begin the molt as much as a month apart, whereas members of the same litter may vary to some extent in the rate of molting but usually begin and end within a week or two of each other. The juvenile molt may be completed more rapidly than either of the other annual molts. Two 13 week old captives began molting July 7. The molt on the body was complete July 20 and the tail fur was fully replaced by August 10. Young of another litter took about 29 days to replace the body pelage and two more weeks to molt the tail.

HABITATS

Sufficient food seems to be the primary habitat requirement of the red squirrel, for it is fairly non-specific in its nesting requirements and can adapt itself to various types of cover. Since the habitats in which it was collected or observed during the study were numerous and often varied only subtly, they are difficult to classify into exclusive categories.

However, about seven fairly distinctive types can be recognized: 1) beech, maple, hemlock forests, 2) mixed hardwoods and scattered conifers, 3) coniferous plantations, 4) old orchards, 5) hedgerows, 6) park-like areas, and 7) edificearian. Each of these at times may support high squirrel populations but, because of barriers which may limit access by squirrels or effects of local conditions on the quantities of food produced, considerable variation in carrying capacities is encountered within and between types.

Mature ungrazed beech, maple, hemlock woods or stands of mixed hardwoods, predominately oak-hickory, with scattered clumps or single trees of white pine or hemlock rank as the most stable habitats, but not always those supporting the greatest numbers. Where hemlocks dominate associations bordering the cool, deep ravines of the region or occur in "islands" dispersed amongst hardwoods, red squirrels exhibit a tendency to aggregate within or near them, although suitable den sites and food supplies may be generally distributed. This inclination has also been noted by Sherman (1936) and others and is probably an expression of an inherent predilection for coniferous cover or seeds.

In other habitats, the distribution of squirrels seems more sporadic and populations more subject to variation. There are too few extensive mature conifer plantations in the region to rank as an important habitat. Squirrels may repair to older stands of red, white, or Scotch pine and Norway or white spruce for feeding, but there is little evidence that many inhabit plantations exclusively. Abandoned apple orchards with an abundance of nest cavities or festoons of grape vines to provide sites for outside nests often support a few squirrels throughout the year, particularly if the food supply is augmented by other fruit or mast producing vines, shrubs, or trees. High fall populations, in response to a good apple crop, have been observed in some orchards.

Hedgerows not only serve as important travel lanes but also frequently support a resident population of their own. Linduska (1950) found a significant percentage of the red squirrel population on study areas in Michigan living in fencerows or similar environments and suggested that such low capacity habitats had survival value in that inhabitants of these discontinuous units of cover might be less vulnerable to epizootics or other factors that might effect more drastic reductions in higher woodland populations. During the winter, hedgerows adjacent to cornfields are often occupied by large numbers of squirrels, inhabiting old woodchuck or chipmunk burrows, or crevices in rock piles and old stumps. In some of these areas, production of natural foods is not sufficient to maintain the high density, and when the corn supply is exhausted they may become virtually devoid of squirrels in a short time.

The Cornell University campus and some cemeteries and residential areas exemplify the park-like habitat. Their wide expanses of lawns and more or less evenly spaced large shade trees and numerous

smaller trees and shrubs frequently support substantial local populations. Circumscribed areas around barns or other farm outbuildings, cabins, and town residences may be sporadically inhabited, often in the fall or winter when squirrels may be attracted by stored grain or bearing nut trees. A single individual was once discovered in a barn that was completely isolated from the nearest hedgerow or woodland by hundreds of yards of open cultivated fields. Squirrels were also noted in a variety of miscellaneous situations, including single or isolated groups of oaks, hickories, or white pines in open fields or along roadsides, thinly wooded culverts, and swales or brushy areas with dense herbaceous ground cover and widely scattered small trees. In winter their tracks were seen in alder thickets along a slow moving stream, and one was caught in a muskrat trap set in a marshy area beside a creek.

Red squirrels appear more adaptable in their habitat requirements than gray squirrels, with whom they are commonly associated. Observations on winter feeding of both species in a hedgerow bordering a cornfield afford an example. Whereas the majority of reds took up residence in burrows or stone piles within the hedgerow, usually 50 to 100 ft from the edge of the corn, the numerous grays who also foraged in the field invariably traveled back and forth along the hedgerow from a woods 1/8 mi. distant. Gifford & Whitebread (1951) commonly found reds occupying submarginal lands in areas where they occurred with grays and were under the impression that the two species did not freely intermix, implying that the reds were forced into the poorer habitats. In central New York, the evidence points to the fact that reds may occupy poorer habitats by virtue of their greater versatility in certain respects and not as a result of interspecific competition.

NUMBERS

Red squirrel populations exhibit seasonal, yearly, and regional fluctuations within various habitats. Seton (1909) considered a squirrel per three acres as abundance for the species. Klugh (1927) estimated the average density of squirrels in the original beech-maple and pine forests of Ontario as one squirrel per 20 acres, and in the spruce woods of New Brunswick as two per 100 yards square. Hatt (1929) recorded a population of 1.8 squirrels per acre on a 10 acre stand of mature red spruce. He estimated squirrel numbers ranging from .2 to .7 per acre in white pine and hemlock forests, spruce swamp, and mixed pine, hemlock, and transition hardwoods. Bole (1939), through quadrat trapping studies, records peak numbers of 1.7 per acre in beech-maple forests of Ohio. Nine family groups, approximating 44 individuals, were counted by Hamilton (1939) on about 30 acres. He found six squirrels living in a three acre oak and maple woodland and eight others occupying a .5 acre oak grove. Densities varying from .31 to .69 per acre were calculated by means of "tagging-return" ratios by Linduska (1950) in oak-hickory woodlots totalling

102 acres. Williams (1936) recorded fall populations of .31, .23, .31, and .50 per acre on a 65 acre tract of beech-maple woods during a four year period. Baumgartner (1938) estimated 2.5 red squirrels per 100 acres of pastured woodlands and 34.4 per 100 acres in nonpastured habitats in Ohio. Unusual concentrations are noted by Klugh (1927) and Seton (1929). The former counted 17 individuals in a group of five butternuts in early September. Seton cites one instance of 14 squirrels being killed on about an acre of wooded land and another in which 15 were killed on a wooded lot less than .5 acre.

Relative abundance of red squirrels in a given area can be fairly accurately assessed by one who is familiar with the habits and signs of the species. The numbers of squirrels seen or heard within a given time interval, usually during a peak activity period, or the numbers of tracks, midden heaps, or diggings observed within a certain area or along a linear distance prove useful as indices of relative population levels. Leaf nest counts are of little or no value in central New York, since the majority of squirrels inhabit tree dens.

Estimates of the actual numbers of squirrels on ten areas were obtained by live trapping or shooting and snap trapping the population. While it was often not possible to take the entire population, the majority could be marked or killed and an accurate estimate made of the number remaining unmarked or surviving. Seasonal variation in trapability was encountered in some habitats. Squirrels were usually live trapped most readily in the winter or early spring when they foraged extensively on the ground. In a woodlot with a fairly stable population of about 20 individuals, a catch of one squirrel per 1.9 trap days in January 1951 dropped to one squirrel per 24.8 trap days in August 1952. Intensive shooting and snap trapping is thought to yield fairly accurate data concerning numbers if conducted in isolated habitats where influx of new squirrels is prevented or restricted, and where it can be accomplished in a short time interval. From late fall to early spring, when populations are most stable and most vulnerable to collecting, appears to be the period when the most reliable results are obtained.

Where small populations exist, individuals can sometimes be counted by direct observation. This method is not feasible when squirrels are more abundant, since duplication is sure to occur. Moreover, it may not be possible to observe more than a fraction of the actual number residing on the area. The extent of such inaccuracies was suggested during observations on 29 marked squirrels inhabiting the Cornell campus study area of about 47 acres, where observational conditions were considerably better than under most field circumstances. During two dawn to dark activity censuses in which the number of squirrels seen on the area was recorded for each hour, individuals were known to move distances up to a thousand feet within a few minutes of the previous observation and certainly would have been recounted if unmarked. The highest number of

squirrels seen during any hourly circuit of the area was 17, about 58% of the actual population.

Populations of 1.85, .96, and .72 squirrels per acre were obtained in three woodlots of mixed hardwoods, hemlock, and white pine totalling 56.8 acres. During January 1951, 10 males and 9 females were live trapped on a 10.3 acre tract of mature ungrazed woodland bordering the Cascadilla Creek gorge on the Cornell University campus. Calculating the population by means of the "Lincoln Index" gave an estimate of 22 squirrels for the same period. Thirty individuals were trapped and released here from January to March 1951. Five females and 3 males were retaken the following year, and 2 females and a male in 1953. Intensive hunting on 23 acres of ungrazed mature woodland produced 10 males, 8 adult females, and 2 subadult females from January 29 to April 15, 1953. At the end of the period, 2 squirrels were known to be left on the area. The woodlot was bordered on three sides by inhospitable environments and no "drift" of new squirrels into the area was detected. A 14.7 acre portion of the woodlot was selectively logged for large white oaks just previous to collecting. The piles of slash and fallen trees attracted foraging squirrels but no other effect of the lumbering on the population was noted. Nine adults (5 males, 4 females) and 8 subadults (3 males, 5 females) were taken from a wooded ravine of 23.6 acres in the period September 16 to October 13, 1951. The woods were mostly climax beech-maple-hemlock with scattered basswood, American elm, hop hornbeam, black cherry, and white pine and were isolated from other suitable habitats by cultivated fields and pastures. Cattle had access to the area but it was little grazed or trodden. The population apparently did not recover rapidly. During March 1953 a careful search was made for squirrel activity, but signs and tracks of only three individuals were found on the area.

The lowest population specifically studied was .28 squirrels per acre. The area was a 10.5 acre woodlot of small second growth beech, sugar maple, and hemlock and was heavily grazed and trodden by cattle. In 156 trap days between July 12 and July 21, 1952, only 2 adult squirrels were taken by live trapping; a third was seen on the last day of the trapping period. The population of chipmunks was 2.19 per acre. No gray squirrels were seen.

Home range studies were conducted on a 47 acre section of the Cornell University campus during the early summer of 1952 and 1953. In both years, it is believed that nearly every individual residing wholly or in large part on the study area was taken. The population was .62 squirrels per acre in 1952. Twenty-nine squirrels including 8 adult males, 5 adult females, and 8 juvenile males and 8 juvenile females from four litters were trapped on the area. In 1953 the population was .85 squirrels per acre and was composed of 40 animals (8 adult males, 6 adult females, 22 juvenile males, and 4 juvenile females). The young represented six litters. A yearling and adult female and two adult males were the only

members of the previous year's population that were retrapped. In both years chipmunks were about equal in numbers to red squirrels, while gray squirrels were about half as abundant.

Hunting and trapping a total of approximately 2500 yds. of hedgerows in two areas produced 1.8 and 2.1 squirrels per 100 yds., respectively, during the winter and early spring of 1951-52. The major portions of both hedgerow systems bordered corn fields. They were composed mostly of shagbark hickory, bitternut hickory, white ash, choke cherry, black cherry, staghorn sumac, basswood, white oak, sugar maple, and various shrubs. They varied in width from 5 to 50 ft. but averaged less than 30. Old stumps and stone piles furnished nesting facilities. Nineteen squirrels (7 adult males, 5 adult females, 3 subadult males, and 4 subadult females) were killed in the first area of 1080 yds. from November 27, 1951 to March 9, 1952. In the second area of 1420 yds., 30 were collected, including 14 males, 7 adult females, and 9 subadult females, from January 16 until April 19, 1952. These populations existed primarily on dried corn and were probably considerably higher than natural food production in the hedgerows would ordinarily support. During the same period resident squirrels were much less common or lacking altogether in many hedgerows that were not near corn fields.

Red squirrels occasionally occurred in some numbers around farm buildings or in restricted areas near dwellings. On September 18, 1952, 7 were taken in less than two hours in or near a group of ramshackle outbuildings. They were attracted to this vicinity each fall by nearby groves of walnuts and filberts. Seven grays and 16 reds had been killed by the owner the previous year in this five acre plot. On another farm, a pregnant female and 3 adult males were trapped within a 50 feet square area about an old shed and woodpile. During the winter of 1950-51, 5 adults (2 males and 3 females) were rarely observed more than a few rods from a group of six large hemlocks occupying less than .1 acre near a busy city street.

FOOD HABITS

Probably more has been written concerning the catholic tastes and profligate feeding habits of the red squirrel than any other aspect of its biology. Hatt (1929) presents a detailed résumé of the foods known to be consumed by this species.

In this study field observations provided the principal data relating to the actual kinds of foods eaten. Stomach analyses gave information on the frequency of occurrence and volume of general types of foods such as mast, green plant matter, fungus, and fleshy fruits, but the specific identity of most of the items could not be determined because of their finely comminuted nature. Chitinous insect remains, feathers, small hard seeds, or fruit skins were sometimes recovered from the stomach or intestines. Stomach contents were examined shortly after the animal was killed, and some foods such as corn, apple, fungi,

raspberries, and flesh could be recognized by color, odor, or texture.

Seasonal Food Cycle. The nature of the food exhibits marked seasonal trends (Table 6), but the habitat and availability determine to a large extent the actual food species. Mast was the staple year-round diet but was most important in fall, winter, and early spring. Winter supplies are for the most part gathered from the ground, buried stores, or caches. White oak, red oak, Shagbark hickory, pignut hickory, bitternut hickory, beech, and butternut are the major source. In many habitats, hemlock cones were the staple winter diet, and in certain local situations seeds of tulip trees and sycamores were heavily utilized. The fruits of staghorn and smooth sumac were consumed, and the trunks and branches frequently girdled. Large patches of bark may be removed from the ground or snow level to the upper branches of trees of all sizes. When near the ground, the work is distinguishable from that of rabbits by the fine, herring-bone pattern of narrow tooth marks. Rabbit gnawing is characterized by a rough, chipped appearance, and the incisor marks are broader. Sumac girdling is apparently more prevalent in some years than in others, although the tree does not seem to be merely a "starvation ration" utilized only during marked shortages of other foods. During the winter of 1951-52 it was extensive in many areas in the Ithaca region and elsewhere in the state, being reported from six counties. None of the barking was attributable to the gray squirrel, although this species is also known to girdle trees (Middleton 1931, Hatfield 1937).

Green plant matter and fleshy fruits made up only a minor portion of the winter dietary. The former was seldom represented by more than trace amounts, probably buds, in the stomach. Apple accounted for the large part of the fleshy fruit recorded, although hawthorn fruits, rose hips, dried honeysuckle berries, and fruits of viburnums and dogwoods were consumed when available. Bracket fungi were occasionally eaten.

TABLE 6. Percentage frequency of occurrence of food items in 145 red squirrel stomachs examined from 1951 to 1953 in the Ithaca region.

Month and Number of Stomachs	Mast	Fleshy Fruits	Green Plant Matter	Fungus	Flesh	Insects
January (7).....	85.7	23.5	28.5	0	0	0
February (13).....	100.0	0	15.4	0	0	0
March (10).....	90.0	10.0	30.0	0	0	0
April (8).....	50.0	0	87.5	0	0	0
May (14).....	64.3	14.3	92.8	0	0	0
June (16).....	62.5	50.0	18.8	0	25.0*	6.2
July (18).....	55.6	61.1	5.6	12.5	0	5.5
August (26).....	73.1	24.1	3.8	26.9	0	0
September (15).....	93.3	6.4	6.4	0	0	0
October (7).....	85.7	28.6	14.2	0	0	0
November (6).....	100.0	0	0	0	0	0
December (5).....	80.0	20.0	0	0	0	0
Totals.....	75.2	24.3	23.4	7.1	2.8	1.4

*Same litter of young.

Tree buds and flowers were the major food in April and May, with American elm, sugar, silver, and Norway maples, red oak, and butternut furnishing a large share of such items. Sugar maple flowers are favored. In two areas, on April 25 and 30, and May 1, 1953, ten feeding squirrels were shot and all but one were eating the inflorescences of this species. Earlier in the season, squirrels slit the branches of sugar maples to obtain the sap. December 1 was the earliest date this was noted. The majority of observations on this behavior were made during February and March. An individual observed during July was busily licking shiny patches of a sweet secretion of some insect (aphid?) off the leaves of a pignut hickory. Hatfield (1937) observed a red squirrel clinging to the trunk of a jack pine beneath a sapsucker and licking up the oozing sap.

In summer an extensive array of food substances were exploited in proportion to their availability in various habitats. Elm seeds and the green samaras of sugar, red, silver, and Norway maples were important foods. It was noted that an individual feeding on Norway maple keys could apparently detect the presence or absence of a normal embryo in the halves of the fruit and would bite open only those which contained a fully developed embryo. Fleshy fruits figured prominently in the diet in June and July. Raspberries (*Rubus*) accounted for a large amount. During July, freshly killed squirrels often bore a distinct odor of the berries. Their stomachs would be stained a dark purple, the seeds occurring throughout the digestive tract and in the feces. A variety of other fruits were readily consumed. In late June, I observed as many as five red squirrels, three grays, several chipmunks, and a host of birds feeding at one time on ripening fruits in the upper branches of a small mulberry. A week later not a berry remained on the tree. In the latter part of the summer fungi assumed significant proportions in the diet.

Green cones of white, red, Scotch, Austrian, and pitch pines, Norway and white spruces, Douglas fir, hemlock, arbor vitae, and larch were eaten as soon as they began to develop. Hemlock and white pine are the most important by reason of their greater distribution and abundance; most of the other conifers occur as scattered ornamentals or young plantations. Many squirrels handled in August were smeared with resin from feeding on white pine cones.

Insects accounted for a small proportion of the food consumed in summer. Flesh and feathers of an unidentified nestling in the stomachs of four young of the same litter collected June 15, 1953 were the only direct evidence of predaceous tendencies obtained during the study. O. Meddaugh and A. Lane of Newark Valley and Ithaca, New York, recounted seeing red squirrels kill young robins and catbirds about their homes. Hatt (1929) summarizes records of animal matter in the red squirrel dietary. Additional observations have been made by Hamilton (1934), Roslund (1951), and Dowden *et al.* (1953).

Mast supplies are at their peak in the late summer and fall, and the period is one of greatest food abundance in most habitats. The fruits of a host of trees, including oaks, hickories, maples, butternut, black walnut, beech, horse chestnut, tulip, hawthorn, apples, pear, sumac, hop hornbeam, and a variety of shrubs and vines were consumed, buried, and cached. Many nuts are still green when eaten or stored. Squirrels taken from late August to October were often stained on the lips and fore feet with brown nut juice.

Feeding Periods and Daily Requirements. Weights were obtained of the stomach contents of 155 specimens, for which the exact time of collection was known. The series covered all hours of the day from 5 a.m. to 8 p.m. Thirteen stomachs (8.4%) were empty or contained only traces of food. The mean weights of the contents of 78 male and 62 female stomachs were 6.1 and 8.5 gms, respectively. The average weights of the stomach contents plotted against the hour of collection indicate that there are probably two main feeding periods during the day. The weights rise from an average of 2.9 gms during the hour between 5 and 6 a.m. to a late morning peak of 8.4 gms between 10 a.m. and 12 noon. The interval from noon to 3 p.m. is poorly sampled; seven stomach contents averaged 6.6 gms. The weights increase after 4 p.m., and the second peak (9.6 gms) is reached between 5 and 7 p.m. Observed feeding activity is in essential agreement except that the most intensive feeding and foraging activity in the morning occurs earlier than the peak stomach weights. The discrepancy in the afternoon is less.

The heaviest 10% of the stomach contents that were weighed averaged 19.0 gms (14.0-25.4). Assuming two feeding periods a day, a rough estimate of the daily weight of food ingested would be 40 gms, or approximately 20% of the body weight. The dry weight of shelled corn consumed by two captive adults over seven 24 hour periods and two 48 hour intervals was determined. The average amount eaten per day was 14.2 gms (6.6-32.3) for the 24 hour periods and 12.6 gms (19.5, 30.9) over the 48 hour periods. These figures probably represent close to the minimum daily consumption since the animals were confined to fairly small cages and were relatively inactive during most of the day. Yeager (1937) assumed that about 2 gms of dry spruce seed were eaten per day. This figure seems low, although the actual amount of food consumed daily undoubtedly varies with the nature of the food and the season.

Food Storing. Food caches and gathering and storing activities are discussed by Audubon & Bachman (1849), Merriam (1884), Seton (1909, 1929), Dice (1921), Murie (1927), Klugh (1927), Hatt (1929), Yeager (1937) Clarke (1939), Richmond & Rosland (1949), and others.

Young squirrels only a few days after weaning often attempt to hide surplus food. Adults were seen caching mushrooms, apples, hawthorn fruits, and discarded bread in bushes and trees at heights of five to 40 ft. in August, November, and December. In April, a squirrel was observed hiding a stripped,

partially burned corn cob in a crevice in a fence rail. Caches of butternuts and walnuts were found in holes in trees, wedged into cracks in trunks, or in crotches of large branches, and between partitions of walls in farm buildings. Gathering and burying nuts reaches its greatest intensity in autumn. On September 22, 1952, I watched an adult male for 20 min. as he cut and buried pignut hickory nuts. He worked rapidly in the upper branches of the tree, uttering excited chirps at frequent intervals. After creeping out to the very end of a sagging twig, he would frequently hang by his hind feet to reach and sever a nut with a quick bite. When 25 or 30 nuts had been cut, he would dash down the tree with a single nut, bury it, and return to the tree. After three cutting forays he began to gather and bury the fallen nuts. Many were carried to the base of the tree and there husked before burial, but others were husked at the spot where they had fallen. He buried the nuts only in several fairly circumscribed areas of thick leaf mold within 100 ft. of the tree. The nuts were sometimes stored singly, but more often were deposited in groups. One cache contained ten nuts packed together in two layers in a shallow depression of soil beneath a layer of mold. The squirrel employed fore and hind feet when excavating and would carefully rake over the site with his fore paws upon completing the operation.

Other individuals were seen hiding nuts in lawns with no attempt at excavation, merely pressing the nut into the grass and drawing a little debris over it. Diggings of red squirrels for buried nuts during the winter seemed to be more frequently encountered in friable, highly organic soils than in heavier types. This may be due to easier digging in the frozen ground or may be evidence of a preference for such sites at the time of burial.

Water. Captive animals need water for drinking and it is presumed that this is also a requirement of wild squirrels. At certain times of the year sufficient moisture may be obtained from succulent food. Wild individuals were seen drinking from puddles, and in one area during the summer several were known to visit a large elm at periodic intervals to lap up sap which oozed from a wound in the trunk. This utilization of sap may be of importance during periods when water is not available in the habitat. In winter, captives regularly gnaw the ice in their water dishes or lick up snow to obtain sufficient moisture.

ACTIVITY

The red squirrel is essentially a diurnal form and is active throughout the year. Detailed information bearing on its daily activity rhythm was obtained by censuses conducted on 47 acres of the Cornell University campus on July 6 and November 2, 1952. A population of about 30 animals resided on the area at these times. Both censuses were conducted on days favorable to squirrel activity. The area was covered carefully once an hour and the time at which squirrel

rels were seen and their behavior while under observation were noted. In the intervals shortly before and after dawn and dark, several circuits were made during an hour in order to record the exact time at which the first and last active squirrels were seen. Every effort was made to avoid duplication of observations. There was little possibility of this on July 6 since most of the animals had been previously marked for home range studies.

For purposes of summary the behavior of the squirrels was roughly classified as alimantal (feeding or foraging), social (chasing, fighting, scolding, or giving communication calls), resting (motionless in a tree in one of the typical resting postures) and "active" (moving about in trees or on the ground but not engaged in any specific activity when observed).

Census studies were augmented by numerous field observations on activity at different hours of the day and by records kept of the times at which 263 squirrels were observed or collected during 153 hours of hunting from June 1952 to July 1953.

The effects of season and various climatic factors on squirrel activity were noted as opportunity in the field afforded. A more quantitative expression of the influence of weather, but still not entirely satisfactory, was obtained by calculating the average numbers of squirrels seen or collected per hour during 261 hours of hunting in various kinds of weather throughout the year. Although squirrels were usually hunted during circumstances favorable to their activity, an effort was made to spend a substantial number of hours in the field during weather conditions assumed to be unfavorable.

Results of hunting (Table 7) and censuses (Fig. 4) indicate that the squirrels exhibit two marked daily activity peaks. The most intensive activity occurs within two hours after sunrise and before sunset, although individuals may be abroad during any hour of the day. Similar observations have been made by Hamilton (1939) for this species and by numerous other observers for other tree squirrels. The graphs of activity (Fig. 4) on July 6 and November 2 are similar in shape and in relation to the time of sunrise and sunset. The peak periods are primarily due to more intense alimantal and social activity. On July 6, 35 (67.3%) of the 52 individuals observed between 4 and 9 a.m. were feeding or foraging and 84.2% (16 out of 19) were similarly engaged between 5 and 7:30 p.m. During

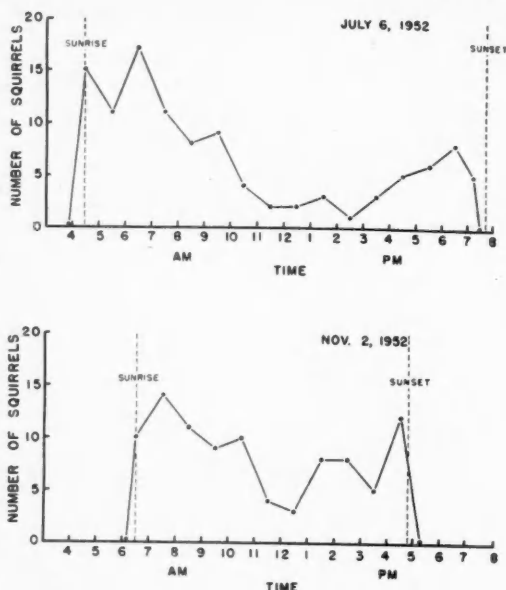


FIG. 4. Red squirrel activity on July 6 and November 2, 1952.

the early morning peak (6-11 a.m.) on November 2, 29 (52.7%) out of 55 were feeding or foraging, and in the late afternoon period (4-6 p.m.) alimantal activity was recorded for 11 (68.8%) of 16 animals observed. Social activity is more pronounced during the early morning period than in the late afternoon peak. Social behavior was noted for 48.1% of the animals seen from 4 to 9 a.m. and for 15.8% of those between 5 and 7:30 p.m. on July 6. On November 2, 24.4% and 12.5% of the morning (6-11 a.m.) and afternoon (4-6 p.m.) peaks, respectively, were due to social activities. Fifty percent of the squirrels seen during the middle of the day (11 a.m. to 4 p.m.) on November 2 were resting, whereas during a similar period (9 a.m. to 5 p.m.) on July 6 only a single resting individual was noted. Since the leaves were largely gone by November, relative visibility probably accounts for a large part of this difference. The remainder of the squirrels noted during these periods were usually feeding or foraging.

The activity period of juveniles for about a month

TABLE 7. Red squirrels seen or collected per hour during 153 hours of hunting from January to November.

	HOURS AFTER SUNRISE							HOURS BEFORE SUNSET						
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-6	6-5	5-4	4-3	3-2	2-1	1-0
Number of Hours Hunted.....	4.0	21.0	32.3	24.5	13.0	7.0	1.5	1.0	3.8	5.8	8.8	13.5	13.0	4.0
Number Seen or Killed.....	14	48	55	36	17	9	0	0	0	9	11	16	29	19
Squirrels Per Hour...	3.5	2.3	1.7	1.5	0.8	0.8	0	0	0	1.6	1.4	1.2	2.2	4.8

after they leave the nest seems to be less markedly bimodal than the adults'. Spring and summer juveniles about 12 to 14 weeks of age were repeatedly observed feeding at all hours of the day on the campus area.

The shape of the activity curves of the gray squirrel (*Sciurus carolinensis leucotis*) and the chipmunk (*Tamias striatus lysteri*) on July 6 and November 2 were essentially similar to that of the red squirrel, although the late afternoon activity period of the chipmunk was much less pronounced than for the other two sciurids. Substantial activity of both gray squirrels and chipmunks did not commence until about an hour after its onset in red squirrels, and also terminated earlier in the evening. The last gray squirrel and chipmunk were seen at 4:31 p.m. on November 2, while reds were active until 5:16.

No habitual nocturnal activity was noted during the study. One individual feeding at a live trap station an hour past sunset on January 12, 1951 afforded the only example of activity after dark in wild individuals. Captives were often active at all hours of the night, summer or winter, and occasionally one would feed only after dark for a week or so following capture. Merriam (1884) indicates that red squirrels may be abroad at night considerably during the autumn, and Seton (1909, 1929) also mentions nocturnal activity in this species.

The impression gained from field experiences is that red squirrels tend to be more active during the middle of the day in fall and winter but are less active at this time during the summer months. Weather conditions influence activity, but the fact that squirrels are more easily stalked or observed under some conditions than others may be a factor in part of the supposed effects of weather. Approximately equal numbers of squirrels were observed or collected per hour on clear and overcast days. They often seemed to be more active during or right after light rain or snow, particularly if there was no wind, but almost all activity ceased during heavy rain or snowfall. Hamilton (1939) observed that squirrels were very active just before snowstorms. A higher percentage of individuals were recorded on days of no or only moderate winds than when strong winds prevailed. Although they were by no means always inactive during high winds they seemed to spend more time on the ground or in sheltered spots and appeared more nervous and wary than ordinarily. During the winter months, fewer squirrels were collected when temperatures were below freezing, although they were often about on the coldest days. The combination of weather conditions that effected the greatest reduction in activity were very low temperatures (0 to 20°F), heavy snowfall, and high winds. At such times few squirrels were active. Even captives in large outdoor cages would not venture from their nest boxes. The animals may remain inactive for two days or longer. On December 11 and 12, 1951 a heavy snow fell. Despite a careful check each day, no squirrels were found active or heard calling until December 13 when the weather

cleared and the temperature rose. Even if the inclement weather persists, however, it is doubtful if the squirrels remain totally inactive for more than a few days, after which they probably come out to forage. During prolonged cold spells it was noted that squirrel tracks and signs of foraging might be absent or scarce for the first several days but then became more numerous again, indicating at least a partial resumption of activity. A warm spell following a period of unfavorable weather often stimulates great activity as evidenced by a maze of new tracks, fresh snow tunnels and food "scrapes," and increased vocalization.

AGE CLASSES AND SEX RATIOS

Age Classes. Nest young, juvenile, and adult were the three main age classes recognized in the study. Individuals from the time of leaving the nest until the onset of sexual maturity were considered as juveniles. When possible these were classified as spring or summer juveniles, primarily on the basis of weight (see growth and development of young). As a matter of convenience fully grown non-parous animals that could not be assigned with certainty to either spring or summer juvenile classes, and whose weights and measurements were equal to those of adults, were referred to as subadults. Such fully developed but sexually immature animals were distinguished from adults, those individuals who had previously bred or were in breeding condition when collected, principally on the basis of the relative development of the genital organs. Certain criteria that proved useful for this purpose during the fall and early winter are presented in Table 8.

Females were comparatively easy to age at all times by the condition of the nipples. Since most adult males had enlarged testes and accessory structures from February to August, no difficulty was encountered in separating juvenile and adult animals during this period, even though the former may equal the adults in weight and measurements by late summer or before. From September to November the reproductive organs of adults were regressed and on cursory inspection appeared similar to the juvenile condition. It was then that the characteristics noted in Table 8 were helpful. In early autumn any single criterion would usually serve to separate the age classes, but a combination of all had generally to be employed later in the season when most adults and many subadults were beginning to approach breeding status. The best single characteristic of the subadult male in early winter was the penile length. This often stamped an animal as a young of the year when the testes, seminal vesicles, and prostate had already commenced to enlarge and were indistinguishable from adults in a similar stage of the sexual cycle.

Sex Ratios. The overall sex ratio of 458 adult and subadult red squirrels collected by all methods was 102 males to 100 females. The proportions of the sexes (104 : 100) of 104 live-trapped animals were not significantly different from those (101 : 100) of

TABLE 8. Criteria useful in distinguishing between adult and juvenile or subadult age classes in fall.

MALES	
Juveniles	Adults
1. Scrotum inconspicuous; a fully haired, shallow sac; no buff or orange colored hairs.	1. Scrotum conspicuous and semipend- ant from December to August; con- dition similar to juvenile in late fall but usually with a patch of buff or rufous hairs on the caudal portion.
2. Length of penis from crus to tip of glans under 50 mm.	2. Penile length over 50 mm; usually exceeds 55 mm.
3. Testes firm; weight of both 50-150 mgs; length usually less than 7.0 mm; tunica smooth and opalescent; its blood vessels with straight edges.	3. Testes when inactive rather flaccid; weight of both over 150 mgs; length exceeding 7.0 mm, usually over 8.0 mm; tunica thick and wrinkled, dull; its blood vessels with crenate margins.
4. Seminal vesicles small and compact; under 10 mm in length.	4. Seminal vesicles when fully re- gressed exceeding 10 mm; flaccid and diffuse.
5. Prostate small; less than 5.0 mm in length.	5. Prostate when fully regressed more than 5.0 mm, usually exceeding 6.0 mm.
FEMALES	
1. Nipples tiny and hidden in ventral fur, mere pimples; less than .5 mm high.	1. Nipples conspicuous, even when in- active easily seen when fur is parted; often black tipped or dusky at base; exceed 1 mm in length.
2. Reproductive tract slender and opaque white; diameter of vagina averaging 1.4 mm from August to December, usually less than 2.0 mm; width of uteri averaging 1.2 mm from August to December, usually less than 1.5 mm.	2. Reproductive tract flaccid, often appearing somewhat translucent; vaginal width averaging 2.7 mm from August to December, usually more than 2.0 mm; width of uteri averaging 2.2 mm from August to December, usually exceeding 1.5 mm.

354 specimens collected by shooting, snap trapping, or road kills. A preponderance of males over females for the juvenile age class is evidenced in both live trapping and kill data. The sex ratio of 92 juveniles collected by all methods was 188 males to 100 females. Thirty-three males and 11 females were taken by live trapping and 27 males and 21 females by shooting or other methods. The marked disproportion in the first instance results from an unexplained predominance of males among the juveniles trapped on the campus area in July and August 1953, when only 4 females were taken as compared to 22 males.

The balance of the sexes of 42 nest young representing nine litters is similarly in favor of the males (23 males to 19 females). Of 13 fetuses in which the sex could be determined, 6 were males and 7 were females.

GROSS SEASONAL CHANGES IN THE REPRODUCTIVE TRACT

Anatomical studies of the reproductive systems of the male and female red squirrel have been made by Mossman *et al.* (1932) and Mossman (1940). The reproductive organs of both sexes undergo distinct seasonal variation. Familiarity with the gross appearance of these structures throughout the year is essential in order to interpret the various stages of the sexual cycle, determine the breeding seasons of

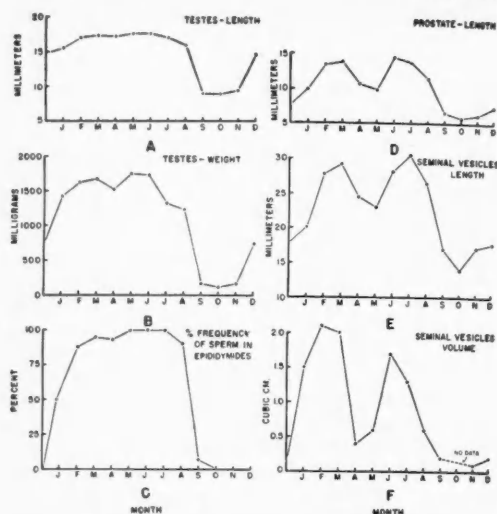


FIG. 5. Seasonal variation in the male reproductive organs. A. Mean monthly testes lengths of 154 adults. 10-27 specimens examined each month except October (3), November (8), and December (6). B. Mean monthly testes weights of 143 adults. 10-23 specimens examined each month except June (9), October (3), November (8), and December (8). C. Monthly percentage frequencies of sperm in the cauda epididymides of 180 adults. 11-20 examined each month except December (8). D. Mean monthly length of the prostate gland of 151 adults. 10-22 specimens examined each month except October (3), November (9), and December (9). E. Mean monthly lengths of the seminal vesicles of 143 adults. 11-22 examined in each month except October (3), November (8), and December (7). F. Mean monthly volumes of the seminal vesicles of 128 adults. 11-20 specimens examined each month except January (8), September (8), October (1), November (6), and December (5).

both sexes, and as an aid in separating immature and adult animals at certain times of the year.

Male. The testes of adults were inactive from September through November and were flaccid and noticeably shrunken. The tunica albuginea was thick and dull colored and its surface blood vessels, wrinkled. The testes averaged 9.0 mm in length and 170 mgs in weight. In the same period, the gonads of subadults were firm; the tunica was taut and had a glistening opalescent color. The blood vessels were narrow and straight. The paired organs weighed between 40 and 100 mgs and measured 5.0 to 7.0 mm in length. A November specimen had testes weighing 250 mgs, but they were obviously enlarging.

The testes of most adults and many subadults showed incipient enlargement in late November and early December (Fig. 5 A and B). In February, 23 of the 27 males collected had the testes fully developed (15 or more mm in length and weighing 1000 mgs or more). A specimen collected April 7 had testes measuring 10.5 x 4.5 mm and weighing 200

mgs. All other males, excluding juveniles born in the spring and summer, had enlarged and heavy testes, averaging 17.4 mm long and 1600 mgs, from March until the latter part of August. During September the gonads regressed to the quiescent state. The curve of mean testes weights (Fig. 5 B) shows a slight decline in April that may be indicative of somewhat reduced spermatogenic activity. The rate of increase in testicular weight in winter appeared to be somewhat slower than the corresponding growth in length. In fall, gonadal weights declined more rapidly than the linear dimensions.

During the periods of enlargement and regression of the gonads the presence or absence of sperm in the cauda epididymis was determined by microscopic examination of fresh smears. At other times the size of the epididymal tubules was an infallible indication of the presence of sperm. When the tubules are clearly visible to the naked eye abundant sperm is invariably present. The presence of sperm is also indicated when a copious amount of viscous fluid exudes from the tubules when they are severed. When sperm is not present in quantity only a small amount of thin watery liquid can be forced from the tubules.

The percentage frequency of the presence of sperm in the cauda epididymides (Fig. 5 C) was closely correlated with testes length and weight. The first occurrence of sperm in the winter was January 19. The last fall record was September 13. Spermatozoa were contained in the cauda epididymis of 116 specimens necropsied between these dates. With four exceptions, the testes of these animals were 15 mm or longer and weighed over 1000 mgs. Two specimens, collected June 21 and July 18, had testes measuring 14 mm and weighing 1200 and 850 mgs, respectively. The epididymides of both were full of sperm. A specimen collected August 18 had a few sperm in the epididymis but the tubules were not macroscopically visible. The gonads measured 11.5 x 5.5 mm and weighed 400 mgs. Another individual shot September 13 had testes 14.0 x 8.0 mm and weighing 850 mgs. The distended cauda epididymal tubules contained abundant sperm. In the last two cases it seems probable that the spermatogenic activity of the testes had ceased, while sperm stored in the cauda epididymis had persisted.

Scrotal condition reflects the relative development of the testes. In many individuals it became conspicuous and semi-pendant during December and January. The guard hairs on the caudal portion became sparse, exposing a dense coating of wooly underfur. There appeared to be no observable difference in the degree of scrotal furring between old adults and sexually active young of the previous breeding season. By June, following the spring molt, the majority of adults possessed a naked patch of black rugose skin on the caudal extremity of the scrotum. This condition persisted until the genitals regressed in September and the scrotum again became fully haired and much reduced. At this time it was indistinguishable from the juvenile condition except

for the usual occurrence of a patch of buff or rufous colored hairs on the posterior part. The testes normally occupy the scrotum at three or four months of age and are probably not again retracted into the abdomen except due to excitement or handling. Enlarged testes can be forced into the abdomen through the inguinal canal. They are often retracted when live trapped males are examined and must be palpated into the scrotum to get an estimation of their size.

The relative size of the prostate gland and seminal vesicles are useful criteria by which to judge the sexual condition of the males of some species (Jameison 1950). The prostate of the red squirrel is an egg-shaped structure partly enclosing the dorsal surface of the urethra just caudad of the juncture of the deferent ducts. Its length was measured along the midline. During the male anestrus the prostate averaged 6.3 mm in adults (Fig. 6 C) and 5.0 mm or less in juveniles (Fig. 6 A). Its surface was smooth in both age classes. Enlargement was noted in late December and January (Fig. 5 D). In most males the gland had attained maximum size (10-18 mm) by February and March (Fig. 6 B). Definite lobules composed of distended tubules became visible on the surface of prostates which had reached a size of 10 mm or more. In no case was sperm contained in the epididymis when the prostatic length was under 10 mm. Size increase in the prostate was initiated later than testicular development. Apparently the former reached functional size rapidly, since few specimens were taken with intermediate sized glands. A noticeable decline occurred in mean prostatic length in April and May, and in many examples the lobes and tubules were faint or invisible. After enlarging again during the summer breeding period, in late June and early July, the glands underwent regression, reaching an inactive condition in most males by September.

The paired, tubular seminal vesicles extend cephalad from the anterior edge of the prostate. When fully enlarged, they can be seen to consist of a large proximal portion composed of large tubules and a smaller distal portion of finer tubules. This terminal portion is retroflexed and lies dorsolateral to the proximal part. The length of the fresh vesicle, *in situ*, was measured from the base of the gland, at the cephalic end of the prostate, to its most anterolateral extension. Care was exercised not to stretch or otherwise distort it. The volume of both seminal vesicles preserved in 10% formalin was determined by water displacement in a graduated cylinder calibrated to .2 ml.

The seminal vesicles (Fig. 5 E and F) exhibit the most pronounced variation of any of the male reproductive organs. From early September until November they were undeveloped. They averaged 16 mm (11-24) long and .2 ml (.1-.3) in volume in adults and were distinctly flaccid and diffuse (Fig. 6 C). In subadults, the seminal vesicles were compact and usually firm, averaging 6 mm (4-9) in length and about .05 ml in volume (Fig. 6 A). Enlargement

was closely correlated with that of the prostate, beginning in late December and January. During the period of vesicular development sperm were present in the cauda epididymis when the vesicles exceeded 18 mm in length. Turgidity accompanied increase in gland size. The large tubules attained a diameter of 2 to 4 mm and were engorged with a clear viscous liquid (Fig. 6 B).

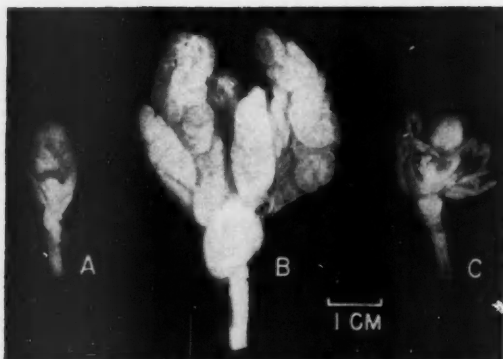


FIG. 6. Appearance of the prostate gland and seminal vesicles at different stages in the reproductive cycle. A. Subadult in fall. B. Adult in breeding condition. C. Adult in post breeding condition in fall.

Two peaks in size and turgidity occurred, the first in February and March and the second in June and July. The vesicles were partially regressed in April and May. During these months the majority of adults had the vesicles still enlarged but extremely flaccid. The tubules were limp and collapsed and contained little fluid. The decrease in volume was more marked than the corresponding reduction in length and quantitatively reflected the actual condition of the glands more accurately. Some evidence suggests that the seminal vesicles lose their turgidity following mating, probably due to the discharge of the contents during coitus. The seminal vesicles of a male shot from a den on February 19, 1953 with a female who had recently copulated, as indicated by sperm in the vagina, were very limp. On July 7, 1953, a pair were observed copulating and killed. The male had flaccid vesicles. Other males collected during these periods had the glands either turgid or similarly flabby.

Following the summer breeding period, the seminal vesicles began to decline rapidly in volume, less so in size, until they reached the inactive state in September.

Female. The genital organs of most adults and all young of the current breeding season were quiescent from August to December. The anestrus adult tract (Fig. 7 B) is larger, more flaccid, and somewhat translucent. The vascularization of the uterus and ligamentum latum is more distinct. The coiled nature of the vagina is hardly evident. Vaginal diameter (measured just below the cervix) of 32 specimens collected from August to December averaged 2.7 mm (1.8-6.0). The mean uterine width was 2.2 mm (1.3-

5.2). Mean length of the vagina and uteri of four adult individuals in late fall was 31.2 mm (28-33) and 26 mm (24-31), respectively. All measurements were of fresh specimens. Corpora lutea and placental scars of the previous breeding season were often visible until late December and early January. December 30 was the latest date the former were definitely recorded by macroscopic examination. Placental sites apparently persist longer; faint scars were detected in one individual on February 9, 1952, almost four months after the close of the reproductive season.

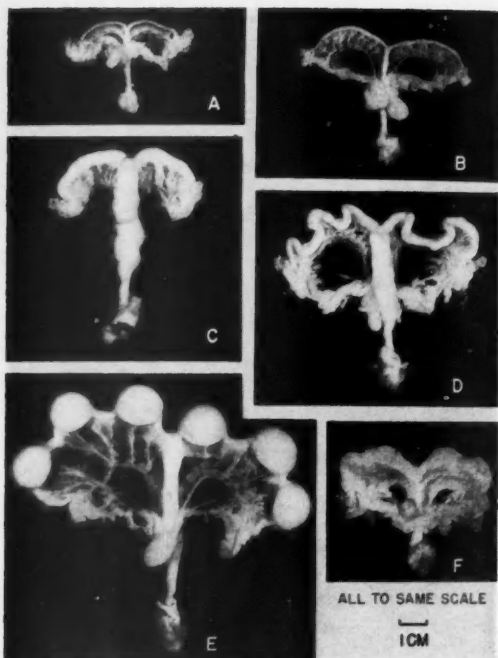


FIG. 7. Appearance of the female reproductive tract at different stages in the reproductive cycle. A. Subadult in fall. B. Adult in fall. C. Estrus condition. D. Early pregnancy. E. Advanced pregnancy. F. Less than one week post partum.

The nulliparous reproductive tract (Fig. 7 A) can be easily recognized. It is small, slender, and opaque white. Uterine blood vessels are faint. The vaginal coils are slightly more distinct than in the anestrus adult. The width of the vagina of 29 specimens examined from August to December averaged 1.4 mm (1.0-3.0); the width of the uteri averaged 1.2 mm (1.0-1.9). The mean vaginal length of four subadults was 22.2 mm (20-26). Average uterine length was 16.5 mm (13-19).

No apparent difference in size or condition of the external genitalia is noted between sexually inactive adults and immature individuals. In both, the lips of the vulva are usually adherent for their caudal two-thirds. A similar condition has been reported for the prairie dog, *Cynomys leucurus* (Stockard

1935) and fox squirrel, *Sciurus niger rufiventer* (Allen 1942).

The teats offer the best external evidence of maturity. They are about the size of an ordinary pin head in subadults and are usually difficult to locate beneath the fur. Females who have previously nursed have conspicuous nipples that are usually more than 2 mm long. If a litter has been recently suckled the nipples are visible without parting the hairs. They are 3 to 5 mm long and pinkish-gray in color except for black apices. The fur surrounding each teat may be matted or sparser than on the rest of the venter. Following lactation the nipples become rather heavily cornified. In the fall, the mammae of individuals that have apparently born only a spring litter are smaller than those of summer bred adults. They are concealed beneath the fur and are whitish in color with only faint pigmentation at the tips.

The reproductive structures of many adults and some subadults showed signs of enlargement in January. During this month a gradual increase in the size and turgidity of the tubal structures occurred. The coiled nature of the vagina became distinct and developing follicles appeared on the erstwhile smooth ovarian surface. Peak periods of estrus occurred in February and March and in June and July (Fig. 8 B). The external sign of heat is the swollen vulva, which may measure 7 x 6 x 10 mm in height, width, and length, respectively. The hairs growing on the urogenital papilla become directed perpendicular to its surface, presenting a coronal effect. In individuals considered to be in the estrus phase, the vagina is markedly enlarged and turgid, projecting cephalad beyond the border of the pelvis almost to the level of the kidneys (Fig. 7 C). The cephalic part attains a diameter of 8 to 11 mm, and the coils are swollen and distinct. The uteri are firm and circular in cross section, their diameter equalling 2 or 3 mm, and they tend to spiral caudad from their juncture with the vagina. Large follicles, visible as clear, hemispherical vesicles about 1 mm in diameter, have been noted in the ovaries when the tract was only partially enlarged. The majority of the females classified as being in estrus were actually in a post ovulatory phase, the ovarian surface showing only recently formed corpora lutea and numerous small follicles. The former appear as opaque, somewhat granular, pinkish areas about 1 mm in diameter.

Subsequent to copulation the vagina undergoes rapid involution. Its walls become thin and somewhat flaccid and the coils indistinct (Fig. 7 D). This change apparently results in enlargement of the lumen to facilitate passage of the fetus at birth. Two females that were killed soon after coitus showed incipient regression of the vagina, indicating that the change may be initiated within a day or two following mating.

Pregnancies occurred from February to September (Fig. 8 C). The gestation period of the red squirrel is not definitely known. Hamilton (1939) estimated the period as about 40 days. He assumed

that it was probably somewhat less than the average 44 day period determined for captive gray squirrels by Lillian D. Powers by reason of the red squirrel's smaller size. My attempts to breed red squirrels in captivity to determine the actual duration of gestation were unsuccessful. Only a few abortive mating attempts were observed among experimental animals housed in large (15 x 15 x 15 ft.) outdoor cages and fed a principal diet of shelled whole corn supplemented by their natural foods.

The smallest uterine swellings observed measured 4 mm and were obtained from a female killed February 22, 1953. Brown & Yeager (1945) state that 3 mm fetal nodes appear in gray and fox squirrel uteri about 10 days after successful coitus. This may occur slightly earlier in the red squirrel. During pregnancy the genital tract remains enlarged but the vagina is flaccid and its coils are not visible or else quite indistinct (Fig. 7 E). The corpora lutea become somewhat better defined and darker colored as gestation proceeds. The nipples increase in size and turgidity, the two posterior pairs usually exhibiting better development than the thoracic and pectoral ones. A clear liquid, presumably the colostrum, can occasionally be squeezed from the teats shortly before partus. During gestation the lips of the vulva may be either sealed or open, but the latter condition obtains most frequently.

Changes in the pelvis occur during the course of pregnancy. Relaxation of the symphysis to increase the pelvic outlet at partum apparently commences in early pregnancy and the two innominates may not re-ankylose until a week or more after birth. Nineteen pelvic girdles that were cleaned by dermestid beetles showed various stages of separation at the symphysis. In many of the specimens the two halves of the girdle were completely separated but in life were undoubtedly joined by a band of cartilage. The pelvis of one specimen in early pregnancy (5 mm uterine swellings) had the symphyseal suture distinct and apparently in an initial stage of resorption. The symphysis was partly open in females with 17 and 20 mm uterine swellings and narrowly open in an individual with 15 mm swellings. The innominates had completely separated in two squirrels carrying nearly full term fetuses and in two collected within a day or two after parturition. The symphysis of a female who produced young in captivity was widely open when the animal was killed eight days later. Several lactating specimens who were taken with the pelvic bones still separated or only partly fused were estimated to have dropped the young about two weeks earlier.

The recent partum reproductive tract (Fig. 7 F) is strongly contracted and thick-walled. The uteri, and to a lesser extent the vagina, are marked by prominent longitudinal striae. Placental sites are not distinct externally but are indicated as slightly enlarged and spongy areas along the length of the uterus. The genital tract of a female eight days after birth of the young had partially returned to the normal state. The uteri and vagina were notice-

ably shorter and narrower and the striae less distinct than in individuals who had apparently borne litters within a day or two of being killed.

Nursing females were collected in every month from March to October (Fig. 8 D). Individuals were considered as "lactating" when milk could be expressed from the teats and were denoted as "recent lactating" if no milk was present but the nipples were still fully enlarged and prominent. During the nursing period the lacteal tissue is developed as two thick sheets that extend from the urogenital eminence to the pectoral region of the thorax. They are in contact caudally but diverge at about the anterior margin of the hind limbs and extend cephalad along the nipple line of each side. The tissue is limited to the ventral aspect of the body.

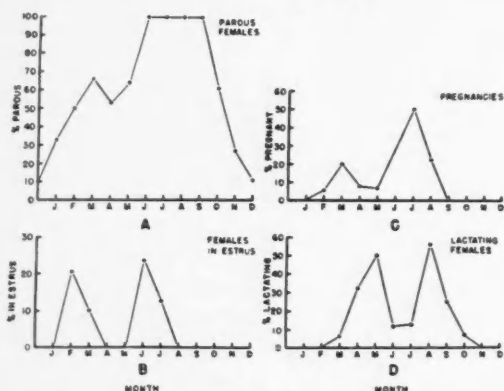


FIG. 8. Seasonal variation in the reproductive condition of females, excluding young of the year from May to September. A. Monthly percentages of parous females in 178 specimens. 11-28 examined each month except August (9) and December (9). B. Monthly percentages of females in estrus in 209 specimens. C. Monthly percentages of pregnant females in 209 specimens. D. Monthly percentages of lactating females in 209 specimens. In B, C, and D, 11-34 specimens examined each month except July (8), August (9), and December (9).

The tubal genitalia of lactating animals are only slightly more developed than during the anestrus phase of the cycle. Placental sites can usually be easily distinguished in fresh uteri that have cleared and returned to the normal condition following parturition. The corpora lutea exhibit a change from the delicate pink structures of the gestation phase to translucent, brownish colored bodies. They also increase in size from 1-1.5 mm to as much as 3 mm and may bulge from the surface of the ovary. It is sometimes possible to distinguish by size and color the two sets of corpora lutea in adults who have borne two litters or are pregnant for the second time of the season.

BREEDING SEASON AND MATING BEHAVIOR

Breeding Season. The breeding season of females was determined from the presence of the estrus con-

dition and by back-calculating from the estimated age of nest or partly grown young, uteri with near term fetuses, or recent partum genital tracts to the approximate time of conception. The condition of the testes and accessory structures were used to assess the reproductive status of males. Field observations of mating chases and actual copulation supplemented these data. The chronology of events is based on information gathered over a relatively short period and may be expected to vary somewhat from one year to another and between different populations and environments.

The season of reproduction extended from January to October. The extreme dates of occurrence of sperm in the cauda epididymis of males were January 19 and September 13. Hamilton (1939) records an individual with active sperm in the epididymis on October 12. Females in estrus were collected between February 4 and July 7. Pregnancies were noted between February 22 and August 14. A gravid female was collected by Hamilton (1939) on September 29. Lactating individuals were taken from March 14 to October 19.

The percentage of females in estrus and the incidence of pregnancy and lactation (Fig. 8 B-D) reveal definite late winter and summer peaks that are indicative of two distinct breeding seasons during the course of the reproductive season. Breeding may take place at other times during the warmer months but apparently much less frequently. Winter matings occurred primarily in February and March and summer breeding in June and July. The incidence of females in estrus is probably the best single criterion of breeding. Estrus females were obtained only in February and March and again in June and July. Ten (15.7%) of the 64 females examined in February and March were in estrus. They were taken between February 4 and March 25. Six were secured during the latter half of February. Of 25 adult females obtained in June and July, five (20.0%) were classified as estrus. These occurred between June 13 and July 7. Assuming a 40 day gestation period, conception of seven spring litters of nest young of known or approximately known age was calculated to have occurred between the first week in February and the first week in April. Estimated dates of conception of one squirrel containing approximately full term fetuses and three within a day or two after parturition were from the first week in February to the third week in March. No summer litters were available for back calculation, but the estimated periods of conception of 24 young collected in October, November, and December and classified as summer juveniles ranged from the third week in April to the second week in August. The calculated conception periods of 17 (71%) of the 24 individuals were in June or July.

The breeding season of the male is less easily determined. If one assumes fecundity to be correlated with the presence of copious sperm in the cauda epididymis, then the reproductive period of males may be considered to extend from January to Sep-

tember and that, as Hamilton (1939) suggests, the females govern the length of the breeding seasons. However, the close correspondence of the developmental peaks of the seminal vesicles and prostate (Fig. 5 D-F) to the female estrus periods (Fig. 8 B) suggest that the breeding season of the male might be more restricted than is ordinarily supposed. The condition of the seminal vesicles and prostate may more accurately reflect a state of physiological or psychological preparedness for mating than the presence of enlarged testes and abundant spermatozoa.

Eight mating chases were observed. Four were recorded between February 19 and March 18, and four from June 15 to July 7. A chase between two individuals was observed on December 30, 1951, during which the male appeared to attempt to mount the female. Both animals were killed and neither proved to be in breeding condition. Hatt (1929) considered that such sporadic attempts at coitus outside the normal breeding season were common.

Mearns (1898), Preble (1908), Dice (1921), Klugh (1927) and Seton (1929) recorded mating activity from February to early April in localities ranging from New York, Ontario, and Manitoba, and northwest to the Athabaska-Mackenzie region of Canada and interior Alaska. They fail to mention a second breeding season in summer. Hatt (1929) considered evidence of breeding in Adirondack squirrels during late July merely as an indication of an extensive breeding season. Hamilton's (1939) observation that breeding occurs during mid-February and early March and again in July agrees with the data presented here.

Mating Behavior. Various authors have conjectured on the permanence of pairing in red squirrels. Walton (1903), Seton (1909), Warren (1910), Cory (1912) and Soper (1942) cite instances of apparent association in pairs at times other than the mating periods. Klugh (1927) found no evidence of association with a mate in the case of a male and female observed singly for more than a year, and Hamilton's (1939) evidence also suggested that the species is promiscuous.

In this study, 13 instances of association between two or more squirrels were recorded. In five cases two or three animals of undetermined sex occupied the same den tree or nest. An instance of a male and female sharing the same tree den was recorded April 28, 1951. Two adult males and a subadult female inhabited a single dead stub in May 1952. On November 22, 1951 an adult male and a subadult female who occupied a tree den and ground burrow about 75 feet apart were shot. Their tracks in the snow indicated that they probably consorted with one another. It was possible to determine the sexes of individuals who composed three small groups commonly associating together in a restricted area. Two adult males and a pregnant female lived together in several old farm sheds during March 1953. Two adult males and a female confined their activity almost entirely to a few large hemlocks in the early winter of 1950. In August 1952 two adult males

and an adult female occupied a farm house attic. On two occasions, in February and March 1952, an adult and immature female were collected from the same nest. Captive animals of the same or opposite sex often shared one nest box and feeding tray but evinced no sign of any attachment to each other.

The heterogeneous nature of these associations leads to the conclusion that there is slight, if any, tendency towards monogamy. Individuals may perhaps form such loose aggregations as a matter of chance or of mutual attraction to a desirable habitat. The occurrence of adult and immature females together may be taken to indicate a possible parent-offspring relationship that had existed through the winter.

The mating chase is a characteristic feature of the breeding activity and a prelude to the actual mating act. The eight chases observed were composed of from two to seven squirrels. In five instances, chases were limited to two or three individuals. Five chases were recorded in the afternoon between 3 and 7 p.m., while the remainder were observed from 5:45 to 8:30 a.m. They occurred either on the ground or in the trees.

Squirrels seemed to locate the main body of the chase through a combination of sight, sound, and smell. An unmistakable feature of the mating chase is a peculiar soft, coughing note that is uttered monotonously by the aroused animals. A similar sound is produced by gray squirrels during their rutting activity. At times of great excitement the anal glands of the squirrels give off a strong musky odor. This specific odor material may also be secreted under the stimulus of breeding activity and serve to guide individuals arriving from outlying areas in the direction of the chase. That this may be true is suggested by the fact that squirrels arriving in the neighborhood of a chase were often observed to sniff about excitedly in trees through which participants of the chase had previously passed.

On two occasions it was possible to kill most of the squirrels involved in a mating chase to ascertain their sex and breeding status. Five males and a female were involved in a chase observed February 19, 1953. Three adult males and an adult female were killed during another chase in the early evening of July 7, 1953. The animals collected during both chases were in full breeding condition.

Only one satisfactory observation was made on actual copulation. While collecting squirrels on July 7, 1953, about 7 p.m., I heard red squirrel mating notes that seemed to come from near the ground. About five minutes later a pair of squirrels in copula appeared at the base of a large white oak about 50 ft. away and began to ascend the tree. They had apparently been mating on the ground. The male was grasping the female about the upper abdomen with his forearms; his head was at the level of her shoulders. He did not release his hold as she carried him up the tree but made sporadic movements of his body that may have been attempts at copulation or climbing. The pair stopped on a dead stub about 40 ft. high and there the male began copulatory at-

tempts. About this time the female took alarm, turned and started for the trunk along the underside of the limb, dragging the male along. The male retained his grasp until they reached the trunk and then scrambled off. Both animals were immediately killed. About three minutes had elapsed during the observation. The vulva of the female was moist with sperm and her reproductive tract was later found to be slightly regressed. The penis of the male was retracted normally but the animal's body was quite rigid, contrary to the invariably relaxed state of a freshly killed specimen.

Several persons have supplied me with additional observations on red squirrel mating behavior. William Werner and Jesse Clovis observed a mating chase and copulation June 11, 1953 on Wellesley Island in the St. Lawrence River, Jefferson County, New York. In this instance coitus took place in a tree and lasted approximately 15 seconds. William J. Hamilton, Jr., contributed two accounts from the vicinity of Ithaca. In late June 1940, a student saw two squirrels chasing through the trees. The male finally overtook the female and mounted her on the ground. They remained paired for 15 minutes, the female carrying the male on her back into a tree for some distance. After the pair separated another male gave chase and attempted to mount the female, but she was not receptive. Hamilton observed mating activity at 3:58 p.m., March 18, 1948. A male coupled with a female was being carried about by the latter. He was thrown vigorously from side to side and lashed his tail about to maintain balance. After dragging her mate about 120 ft. the female halted on an elm limb and copulation occurred. During a burst of conjugal activity, the pair fell from the limb to the ground, a distance of about 45 ft. Neither were harmed and they scurried off to different trees. About a minute later the male climbed the tree in which the female had taken refuge and the two engaged in a fast pursuit in the upper limbs.

FECUNDITY

Size of Litters. The most satisfactory criteria of the number of young produced are considered to be placental scars, embryos, and nest young. Corpora lutea give results that are apparently slightly higher than is actually the case due to the loss of ova through failure to be fertilized or implant. A mean

TABLE 9. Litter size of red squirrels in central New York as indicated by counts of placental scars, embryos, and nest young.

Criteria	SPRING		SUMMER		TOTAL		
	No.	Mean	No.	Mean	No.	Mean	Range
Placental Scars.....	21	3.8	9	5.9	46*	4.7	3-8
Embryos.....	11	4.1	6	4.3	17	4.2	1-6
Nest Young.....	11	4.2	0	0	11	4.2	2-7
Total.....	43	4.0	15	5.3	74	4.5	1-8

*Includes specimens that could not be definitely assigned to spring or summer breeding seasons.

litter size of 4.5 was determined from 74 sets of placental scars, embryos, and nest young (Table 9). Specimens in which the actual number of corpora lutea or placental sites could not be obtained with certainty were excluded from the sample, as were individuals collected from January 1 to early spring who still retained faint traces of corpora lutea or placental sites of the previous season. The slightly higher average number of young produced in summer litters is perhaps not significant due to the small size of the sample from that period, although the number of young per litter has been found to average slightly higher in summer than spring in the fox squirrel (Brown & Yeager 1945) and gray squirrel (Shorten 1951). The mean numbers of placental sites of 46 red squirrels taken in 1951, 1952, and 1953 were 4.4, 5.2, and 3.9, respectively. Records of number of placental scars, embryos, or young given by Mearns (1898), Seton (1909), Swarth (1911), Dice & Sherman (1922), Klugh (1927), Hatt (1929), Svihla (1930), Richmond & Roslund (1949), Grimm & Roberts (1950), and Grimm & Whitebread (1952) from areas representing a substantial portion of the range of this species vary from 2 to 8 with a mean of 4.9.

Comparison of average numbers of corpora lutea and placental sites gives some indication of implantation success. The ovaries of 46 squirrels contained a total of 226 corpora lutea, while 215 placental sites were present in the uteri, indicating about 95% implantation. The loss of ova does not seem excessive. The disposition of the corpora lutea and placental sites in the same series of 46 specimens seemed to be at random with respect to the right and left sides. A single instance of possible migration of an ovum from one uterus to another was noted.

Of 17 pregnant reproductive tracts examined, two contained resorbing embryos. One of two embryos contained by a female collected July 17, 1952 was undergoing regression. A female trapped March 30, 1953 died in captivity April 20 and was found to contain four resorbing embryos. In this instance resorption may have been due to the effects of captivity.

Number of Litters. Poole (1932) and Soper (1942) indicate that red squirrels produce only a single litter each year. Klugh (1927) and Hatt (1929) intimate that second litters are an exception, whereas Lyon (1936), Hamilton (1939), Grimm & Roberts (1950), Linduska (1950), and Grimm & Whitebread (1952) conclude that second broods may actually be of more common occurrence. My data indicate that many adult females probably produce two litters during the season. Five females whose large and prominent teats marked them as having produced young in the spring were approaching breeding condition when collected between June 15 and July 5. On July 30, 1953 a pregnant female who had borne a litter earlier in the year was killed. Examination of individuals killed August 4 and 17 revealed the presence of two definite sets of corpora lutea in the ovaries. In other summer-bred individuals who were shot during

the fall there were occasionally traces of two sets of placental sites or indistinct suggestions of an older set of corpora lutea.

All adults do not bear two litters in a season, and some may not breed until later in the summer. Two females collected June 13 and 20, 1952 were approaching estrus when killed. Although their mammae indicated they had previously produced young, they had apparently not suckled a spring litter. On July 12, 1952 a pregnant adult was killed who evidently had not lactated since the previous reproductive season. A female live trapped as an adult January 1951 and found to be in anestrus when killed March 31, 1953 further indicates that not all old individuals breed during the first peak in February and March.

Spring juveniles of the previous year apparently mature in late winter and breed at that time. Evidence for this is found in the sharp increase of parous females (Fig. 8 A) and the reciprocal decrease in nulliparous animals following the late winter and early spring breeding period. From November to February, 63.3% of 60 females had not previously bred, but from March to June only 29.2% of 72 individuals were non parous. The subadult animals encountered in the latter period are assumed to be the summer juveniles of the preceding season who, together with adults breeding for the first or second time of the season, compose the summer breeding peak. Some yearling summer juveniles may mature in time to breed in spring. All yearlings apparently produce only a single litter during the season regardless of the time at which they mature, although slight evidence is available on this point. A female that had been marked as a spring juvenile on June 13, 1952 was retaken June 22, 1953 and found to be in post breeding condition. She was in anestrus when killed July 25, suggesting that she probably would not have bred again during the summer.

Three parous females were killed in the late summer and fall of 1953 whose skeletal structure indicated them to be young of the current season. They showed no wear on the cheek teeth and had the epiphyseal sutures of the humerus and femur distinctly visible. Included was a female in advanced pregnancy, killed August 14, and two lactating specimens taken September 6 and October 19. These observations seem to indicate that young born early in the season may occasionally mature precociously and breed before the end of their first summer.

Males apparently mature earlier than females. The prevalence of specimens with intermediately developed sexual organs in late winter and early spring make it difficult to differentiate between adults and yearlings who are approaching breeding status. Males that were fecund by the time of the spring breeding season probably included adults, spring juveniles, and perhaps some summer juveniles of the previous year. In February and March, 42 (91.3%) of 46 individuals examined contained sperm in the epididymis. No immature males (excluding young

of the current season) were taken after April 7. The subadults collected from February to early April are assumed to be yearling summer juveniles.

GROWTH AND DEVELOPMENT OF THE YOUNG

In central New York the majority of young are apparently born from late March to early May and from late July to early September, although litters may also be produced at other times during the spring and summer months. Growth and development of 23 nest young of six litters that were born in the wild and reared by hand in the laboratory was studied. They were obtained at ages ranging from an estimated 10 to 56 days and were kept for various periods, some being killed at intervals to obtain data on skeletal development and other features. Their age at capture was calculated on the basis of a study by Svihla (1930), in which the growth of two litters born in captivity and nursed by the mother was described. Age criteria established from Svihla's observations and the study of these hand reared, wild born young were in turn used to estimate ages of individuals shot or live trapped in the field. Shorten (1951) found that pre-weaning growth curves of hand reared gray squirrels did not differ markedly from those of captives nursed by the mother, and that the post-weaning growth curves paralleled each other closely. As far as could be ascertained this was also true of red squirrels when the kinds and amounts of food supplied the animals were carefully controlled.

Condition at Birth. A captive female bore five young on March 29, 1953. One specimen, a female, was removed on the day of birth for a permanent record (Fig. 9). Milk in the stomach indicated that it had nursed. Measurements and descriptive data were recorded before preservation. The remaining young were subsequently abandoned by the parent and died within a day or two.

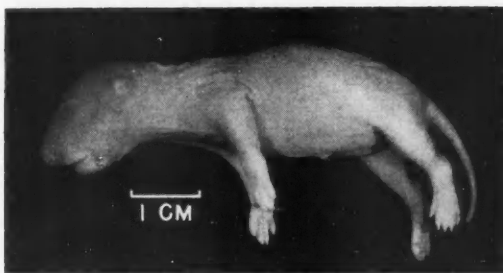


FIG. 9. Red squirrel at birth.

The skin of the new born young is pinkish in color and somewhat rugose. The viscera and the sutures between the frontal and parietal bones of the skull are distinctly visible through the skin. There is no evidence of pigmentation due to developing hair follicles on any part of the body except the anterior edge of the nose. The entire complement of vibrissae are present. The body is otherwise

naked except for numerous fine white hairs on the lips and chin.

The pinna of the ear stands out from the side of the head as a small, unpigmented, fleshy tab that is folded over the ear opening. The external auditory meatus is closed. The eyes are dark areas about 4 mm in diameter and bulge only slightly from the surface of the head. Shallow creases that mark the eventual line of separation of the lids are visible. Well developed claws are present on all digits except the thumb, which bears a blunt nail.

The sex can be determined by the relative distance between the vulva, or penis, and the anus. In the female the urogenital papilla is directly before the anus, whereas in the male a definite hiatus exists between the penis and anal opening. The scrotal fold is also quite apparent. In both sexes the four pairs of nipples appear as tiny, slightly elevated specks lateral to the ventral vibrissae. Measurements of the freshly killed specimen were: total length 70.0 mm, tail 20.0 mm, hind foot 10.5 mm, head 19.0 mm, weight 6.7 gms.

Pelage. The dorsal surface of the body becomes darkly pigmented by the time the young are six or seven days old and hair is visible on the crown and back by the ninth day (Svihla 1930). The age of two nestlings secured on May 28, 1953 was estimated at 10 days. They had a fine coating of blackish hair on the dorsum. It was thickest on the nape and crown, where it had a brownish-red tinge, and sparsest on the limbs. The ultimate pattern on the nose, a dark median bar bordered with light buff areas, was already distinct. The white eye ring was similarly well defined. A thin coat of white hairs was present on the ventral surface.

Subsequent development of the pelage was in accord with Svihla's (1930) observations. At an estimated age of 13 days, the occiput and nape were decidedly more reddish, and a faint rufous stripe extended posteriorly between the shoulders of one individual. The hair on the body was longer and thicker. The area of the lateral stripes was more deeply pigmented than the remainder of the dorsum. At 18 days the rufous middorsal area was visible all along the back. The lateral stripes were distinct and orangish hairs had appeared on the fore limbs and shoulders. The depressed nature of the tail was evident, the hairs being largely confined to the dorsum and lateral margins and measuring about 1/4 in. long.

Three young of a litter of seven obtained April 25, 1951 at an estimated age of 20 days, and two individuals collected May 5, 1953 at approximately 28 days of age provided data on later pelage changes. The lateral stripes and middorsal area were less distinct than earlier when the animals were about 30 to 32 days of age. At this time the tail was becoming more flattened in appearance and measured about 1 cm wide. The black subterminal band of the tail hairs was about 1/8 to 1/4 in. exposed. A week later the entire band had grown out and was separated

from the vertebrae by a buff area nearly 1/4 in. wide. The tail hairs could be voluntarily expanded or appressed to the vertebrae.

Succeeding development of the coat involved merely a lengthening of the guard hairs, resulting in the "fuzzy" appearance of the juvenile animal, growth of prominent ear tufts, and final development of the tail. These changes were largely accomplished by eight weeks of age. The molt of spring juveniles at an age of about 12 to 15 weeks has been described elsewhere.

Eyes and Ears. The eyes of the young of two litters observed by Svihla opened at 27 and 35 days of age. One of the young that I obtained at about 10 days of age had opened its left eye when estimated to be 26 days old. Both eyes were open the following day. Two of three young of another litter had the eyes open in the early evening of the estimated 29th day. The left eye of one had opened that morning. The third individual opened its eyes a day later. The young were seen to scratch the eyes somewhat vigorously just prior to the separation of the lids. The external auditory meatus of two captive young became patent at 18 days of age. Thereafter the squirrels would flinch at a sharp sound, such as the click of a camera shutter.

Skeletal Development. Material representing the earlier stages of skeletal development was obtained from captive individuals killed at various ages (accurate to within two or three days). Beyond seven to eight weeks the series was augmented by juveniles collected in the field and aged according to criteria established from the laboratory raised animals. The skull bones of a new born young were separated by membranous areas. A median fontanelle between the frontal and parietal bones and a larger one at the juncture of the parietals and interparietals were present. The terminal portion of each ramus of the lower jaw was capped by a cartilage 1.8 mm long. A specimen at 18 days had the sutural lines distinct but the skull bones were more or less fused and immovable. The fontanelles had closed. In three specimens estimated at 10 to 11 weeks the sutures between the supra-, ex-, and basioccipitals were indistinct. They were partly obliterated in a 12 to 13 week old individual and completely obsolete in a 13 to 14 week old animal. The interparietal was barely discernible at 12 to 13 weeks and could not be traced in a 13 to 14 week old specimen. The remaining skull sutures apparently remain visible throughout life. Skull measurements from birth to an estimated age of 18 to 19 weeks are given in Table 10.

Neither the upper nor lower incisors are visible at birth, although their respective alveoli were prominent in a dissected skull. The upper incisors of a skull estimated at 18 days measured 3.1 mm from the anterior margin of the alveoli to the tip while the lowers were 5.4 mm. Both pairs were entirely white and peg-like in appearance. There was no apparent distinction between the enamel and dentine

TABLE 10. Average skeletal measurements in millimeters of 25 red squirrels from birth to an estimated 18-19 weeks of age.

Number of Specimens	Estimated Age	Pelvic Length	Humeral Length	Femoral Length	Total Length of Skull	Zygomatic Breadth	Cheek Tooth Row	Mandibular Length
1.....	Birth	8.1	9.0	8.2	17.7	10.3	—	11.4
1.....	18 days	12.2	15.0	15.5	30.0	16.7	—	19.5
2.....	21 "	13.9	15.8	17.0	30.5	16.4	—	20.1
3.....	30-32 "	16.0	18.1	—	33.6	18.0	—	22.1
3.....	38-41 "	16.7	19.2	20.2	35.7	20.1	—	23.5
1.....	7-8 weeks	—	24.0	28.0	38.6	22.0	7.0	26.0
2.....	9-10 "	25.5	25.8	30.4	40.5	22.9	7.3	27.4
3.....	10-11 "	27.3	27.0	32.4	43.4	23.7	7.5	28.0
1.....	12-13 "	30.0	29.5	35.2	43.8	24.0	7.0	28.5
1.....	13-14 "	29.0	28.5	35.5	44.5	24.5	7.5	30.0
2.....	16-17 "	30.2	30.0	36.5	43.5	25.5	7.2	29.5
5.....	18-19 "	32.1	30.1	37.0	44.4	24.4	7.2	29.5

layers and no visible wear. In two estimated 21 day old skulls the upper incisors were 2.3 and 2.7 mm and the lowers 5.4 and 5.5 mm. In one, the very tips of both pairs of incisors had become slightly beveled through wear. At 21 days the lower incisors of three hand reared young protruded about 1 mm above the gum line. The upper pair was not visible.

In two skulls of approximately 30 days the incisors had become slightly yellowish on the frontal surface, except near the tips. Both pairs were noticeably beveled on the inner surface. They measured 2.3 and 2.6 mm and 5.0 and 6.0 mm, respectively. In a 32 day example the teeth were distinctly chisel-shaped and a trace of the pulp cavity was visible on their worn posterior faces. The uppers were 3.6 mm and the lowers 7.7 mm. In 32 day old captives the upper incisors extended from .5 to 1 mm above the gums. The lowers projected about 5 mm. In estimated 38 and 41 day skulls the upper incisors measured 3.5 and 4.2 mm and the lowers 6.7 and 7.2 mm. They were a deeper orange-yellow color than previously. The upper teeth tapered toward the tips.

The sides of the upper incisors of a seven to eight week old animal were parallel throughout their length. They were a deep orange-yellow on the front, and a distinct separation between the enamel and the dentine was apparent. They measured 5.3 mm. The lower pair were more slender, a lighter color, and measured 10.2 mm. Functional incisor length is attained by the age of 12 to 13 weeks. Henceforth, the average length of the upper pair is slightly over 7 mm and that of the lowers approximately 11 mm. Functional milk incisors are apparently lacking, as in most rodents, since no evidence of incisor replacement was noted in the series of 25 skulls examined.

The functional milk premolar (P4) was visible at the surface of the maxillary bone but did not protrude above in the skulls of two individuals about 30 days of age. In 38 and 41 day examples the premolar was just visible above the alveolus in lateral aspect and M1 was at the surface of the jaw. In the lower mandible the deciduous premolar protruded

above the alveolus, m1 was slightly exposed, and m2 had reached the surface. The first three cheek teeth (P4 M1, M2) were fully erupted and in line in a seven to eight weeks skull. M3 was just visible above the bone in lateral view. The four lower cheek teeth protruded above the alveolar surface but m3 was below the level of the others. In two skulls of 9 to 10 week old individuals the last molar in both jaws stood higher than previously but was still not fully aligned with the remainder of the row. In a third example about the same age M3 was only slightly below the level of the other cheek teeth while m3 was fully in line. The last upper molar was aligned with the anterior teeth in a 12 to 13 week old individual.

The deciduous premolars were being replaced in a single specimen estimated at 13 to 14 weeks. In four examples between 16 and 18 weeks the milk premolars were in various stages of being forced out by the growth of the permanent teeth. The upper and lower pairs are apparently replaced at about the same time. The premolars of one specimen estimated at 18 to 19 weeks old were still being replaced, while in three other individuals of the same age the complete permanent dentition was present.

Changes in the crown pattern of the cheek teeth result from wear. In the upper jaw wearing occurs initially on the protocone, exposing a small yellowish crescent of dentine. Further wear enlarges this area and produces dentinal lines on the proto- and meta- and their respective conules. In old adults the surface of the tooth becomes completely flattened or concave and lacks any traces of the former sculpturing except for vestiges of the proto- and meta-conules on the labial side.

A 6 mm section of the diapophysis of the humerus was ossified in a young at birth; the terminal portions were cartilaginous. In an 18 day specimen broad epiphyseal plates were present on the proximal and distal ends. At the former, two ossification centers, representing the head and greater trochanter, were distinct. The separation between these centers was still faintly visible in two skeletons estimated at 38 to 41 days. At this time the epiphyseal sutures

were prominent dark reddish lines and an ossification center that forms the medial epicondyle was visible and separated from the shaft by a prominent suture. In three examples 10 to 11 weeks old the distal epiphyseal suture had largely disappeared, while the proximal epiphyseal and medial epicondylar sutures were still clearly marked. The proximal epiphyseal suture was still visible in juveniles estimated at 18 to 19 weeks, but the condylar suture was faint at about 16 to 17 weeks. The upper epiphyseal suture apparently does not become obsolescent until six or seven months of age. No spring juveniles with visible sutures were collected after December 6. March 22 was the last date that sutures were discernible on presumed summer juveniles. Humeral lengths (Table 10) of 18 to 19 week old juveniles fall within the ranges of adults.

In a new born young, only 4.5 mm of the femoral shaft was ossified. The upper and lower epiphyseal plates were distinct in a specimen at 18 days. The proximal epiphyseal suture was difficult to see at 18 to 19 weeks, but the distal one apparently persists until approximately six or seven months of age. In most spring juveniles collected in November and early December it was absent or barely traceable. During the same period it formed a prominent groove or dark reddish line in many summer juveniles. In addition there were specimens of intermediate condition which could not be definitely assigned to either group by femoral examination. Individuals that were taken in February and March with the sutures still visible were assumed to be summer juveniles. At 18 to 19 weeks femoral length (Table 10) is within the adult range, but average adult measurements are not approximated by spring juveniles until sometime after September. A small series of femurs of summer juveniles averaged smaller than adults until December and January.

The pelvic girdle was almost entirely cartilaginous in a new born individual. An ossification about 2 mm long was present in the ilium, and another about half the size appeared in the ischium. The three pelvic elements were still distinctly separated by cartilaginous areas in a young at 18 days. The ramus of the ischium was unossified and cartilages terminated the ilium and dorsal angle of the ischium. The lower part of the ischial ramus apparently remains cartilaginous until five to six weeks of age. It was completely ossified in a seven to eight weeks skeleton. The sutures between ilium, ischium, pubis, and acetabular bone were visible in a 13 to 14 weeks animal but were not recognizable in two 16 to 17 week old individuals.

The crural tubercles appear at about 16 to 17 weeks. There was no apparent sexual difference up to 19 weeks. The tuberosities were perhaps slightly more enlarged in males exceeding five months but the difference was insufficient to distinguish the sexes. Apparently the full development of these processes in the male occurs at the approach of sexual maturity. A subadult, collected February 22, 1953, whose sexual

structures were in an early stage of enlargement, had fully developed tuberosities.

Measurements of pelvic length from birth to approximately 19 weeks are given in Table 10. The lengths of five 18 to 19 week examples are included within the range of adults, although they average slightly smaller.

Weights and Measurements. Increase in weight of three captive litters comprising six individuals was fairly constant (Table 11). The relative weight increments of one litter decreased slightly after their 12th week. Weights of juveniles killed or live trapped when plotted against the growth of captive litter 3 indicated a similar growth curve for wild young, although the weights were considerably scattered due to individual variation and differences in birth dates. Adult weight is probably not usually attained until sometime after the 18th week of age, although there is considerable variation in this respect. The first spring juvenile of fully adult weight (195.9 gms) was taken August 17, 1952. Summer juveniles of adult weight (more than 170 gms) were not collected until November.

TABLE 11. Average weights in grams of three litters of wild born young that were hand reared in captivity.

LITTER 1 (2 males)		LITTER 2 (1 male, 1 female)		LITTER 3 (2 females)	
Est. Age	Weight	Est. Age	Weight	Est. Age	Weight
10 days	22.9	21 days	31.7	42 days	51.1
14 "	28.2	24 "	31.4	48 "	56.3
19 "	36.0	28 "	35.9	55 "	62.3
21 "	36.8	32 "	39.6	60 "	86.5
25 "	48.4	35 "	46.6	76 "	103.6
		38 "	45.7	84 "	127.8
		42 "	56.1	91 "	130.1
		45 "	57.6	97 "	143.1
		49 "	68.6	104 "	149.3
		56 "	81.4	111 "	144.3
				118 "	153.7
				125 "	157.2

The first wild spring juvenile was killed in May and weighed 79.6 gms. Forty-one juveniles averaged 121.0 gms (85.8-162.7) in June, while the mean of 15 July individuals was 133.7 gms (83.0-168.2). Weights of 12 August specimens varied from 115.4 to 195.9 gms, averaging 155.5 gms. In September, 13 animals weighed from 145.1 to 192.7 gms with a mean of 173.5 gms. Eight individuals, positively identified as spring juveniles by their skeletal structures, collected from October to January averaged 182.4 gms (159.9-204.8).

Summer juveniles were first obtained in October when 11 specimens averaged 132.5 gms (58.8-159.7). In November 13 individuals weighed from 106.4 to 178.9 gms, with a mean of 143.0 gms. Eleven immature specimens recognized as summer young by their skeletal structures were collected from December to February and averaged 158.9 gms (127.4-203.8).

After October a number of fully grown young that probably included both spring and summer juveniles could not be definitely assigned to either age class and were simply designated as subadults. Monthly averages of 59 subadult weights for the eight months from October to May were 173.4, 178.1, 174.4, 188.9, 170.8, 173.0, 166.0, and 205.7 gms, respectively. No consistent increase in weight during this period is apparent from the data.

The estimated ages of wild juveniles were based principally on weight curves of captive young, primarily those of litter 3 (Table 11). Although body weight is probably the most practical single criterion of age in the young animals, its use is subject to a certain amount of error. Individuals exhibit daily fluctuations in weight of as much as 5 gms due to the amount of food in the stomach (which may equal 20% of the body weight) and to an actual gain or loss of weight from day to day. Intra-litter weight differences and those between individuals of the same age were found to range from .9 to 43.3 gms in young from 10 to 118 days of age. Variation in weight is relatively small in nest young but becomes considerably more marked after the young are weaned and begin to forage for themselves.

Average measurements of total length, tail, and hind foot of 28 nest young and juveniles are given in Table 12 and provide an estimate of the absolute and relative growth of the conventional linear measurements from birth to an estimated 19 weeks of age. Measurements for the earlier ages were obtained from captive young. Wild juveniles, aged primarily according to body weight, supplemented the data from hand reared young beyond seven to eight weeks.

TABLE 12. Average measurements in millimeters of 28 nest young and juvenile red squirrels from birth to an estimated 18-19 weeks of age.

Number of Specimens	Estimated Age	Total Length	Tail Length	Hind Foot
1.....	Birth	70.0	20.0	10.5
1.....	18 days	148.0	55.0	28.0
2.....	21 "	156.0	54.0	29.0
2.....	30 "	167.0	64.0	31.5
2.....	38-41 "	182.0	73.0	37.5
1.....	7-8 weeks	236.0	102.0	45.0
2.....	9-10 "	262.0	111.0	47.0
5.....	10-11 "	267.6	113.2	44.4
3.....	11-12 "	282.3	119.3	47.7
2.....	13-14 "	283.5	115.5	46.0
1.....	16-17 "	296.0	127.0	48.0
6.....	18-19 "	299.8	124.8	49.0

Monthly figures for other juveniles killed in the field indicate the general growth increments and variability among wild young during the summer and fall. A spring juvenile taken in May had a total length of 262 mm, tail 111 mm, and hind foot 46 mm. In June, five individuals averaged 267.6 mm (255-281), 111.6 mm (104-116), and 44.0 mm (42-46). Means of 11 July specimens were 287.8 mm (252-308), 122.2 mm (111-136), and 47.6 mm (44-

49). Twelve spring juveniles averaged as large as adults in August. Their measurements were: total length 302.1 mm (278-319), tail 125.7 mm (112-134), and hind foot 48.8 mm (46-51). Subsequent monthly averages were not significantly greater. The mean measurements of 21 individuals collected from September to January were 306.9 mm, 127.2 mm, and 47.7 mm.

In October, 12 summer juveniles averaged 291.8 mm (236-315), 121.3 mm (102-138), and 46.0 mm (42-51). Ten November specimens had a mean total length of 293.9 mm (275-308), tail 123.2 mm (109-131), and hind foot 46.7 mm (46-48). Measurements of three December individuals were 285.7 mm (274-292), 122.0 mm (117-128), and 45.7 mm (44-47). Eight summer juveniles collected in January and February averaged as large as adults. Their mean total, tail, and hind foot lengths were 302.8 mm, 122.1 mm, and 47.0 mm.

The range of monthly mean measurements of 44 subadults collected from October to May were: total length 297.7-311.2 mm, tail 114.0-128.8 mm, hind foot 46.4-48.4. There appears to be no significant trend towards an increase in measurements during this period.

Behavior. The new born young is capable only of feeble twisting and turning movements. Two young about 10 days old were able to sprawl upright with the legs splayed out at right angles to the body. In attempting to move they forced themselves backwards. The tail could be held erect or slightly crooked. Sharp sucking squeaks were uttered when they were disturbed. At 13 days they crawled about more actively, particularly when hungry, and appeared to become restive if one was removed from the nest box. Occasionally they gave a low "churring" sound. When 19 days old they could crawl forwards with fairly good coordination, the legs being held more beneath the body for better support. Body temperature was presumably partly regulated by lying on the back with the limbs extended when overheated or by curling in a tight ball when cool.

Young of a second litter at an estimated 22 days of age were able to scratch an ear with a hind foot and hold the tail up over the back when drinking from an eye dropper. They could cling tenaciously upside down to the hand. With the opening of the eyes, the young began to wash while lying on their sides. When a month old they were extremely active prior to feeding and would climb about over furniture with characteristic squirrel-like hitching movements. At this age they also began to utter a low, rapid, breathless sounding "buzzy" note that was strongly reminiscent of the adult mating sound. They were able to sit up to wash and groom the tail.

Chasing and mock fighting occupied much of the active period when the squirrels were about 38 days old. The litter mates evinced a definite desire to remain together; if one moved off the others would immediately troop after it. Several days later one individual gave the extreme anger note, a sharp rasping cry, when approached by another as it fed. They

began to nibble at solid food at this time, sitting up in true squirrel fashion with the tail lying forward over the back and employing the rudimentary thumb tubercles to manipulate tiny particles of food.

Between six and seven weeks of age the young began to make drumming movements with the hind feet when angry or excited. They also appeared less gregarious. The food storing instinct manifested itself at this time, and they frequently cached articles of food in crevices in the woodwork or furniture. At 53 days one was heard to scold softly. Two days later the male of this family was observed attempting to mate with the females. He would grasp one tightly in the groin region with his fore limbs and nudge her about the neck and shoulders with his head while making copulatory attempts. Such pseudo copulation was also noted between individuals of another litter at about 19 to 20 weeks of age. The paired animals would often fall on their sides during the act, which lasted about 30 seconds. The male invariably took the initiative, yet the female, although apparently uninterested, would submit passively. Similar behavior was observed in June and November among wild juveniles about 11 to 14 weeks old. In one instance two squirrels alternated in mounting each other. Their sexes were not determined. Another time mounting occurred between two seven or eight week old individuals as they foraged on the ground near the den tree.

Weaning. The young are apparently weaned at about seven or eight weeks of age. Individuals of one hand reared litter would occasionally accept solid food after about 38 days of age but did not give up milk entirely until approximately 50 days old. Another litter secured at an estimated age of eight weeks fed on solid foods from the day of capture. A third litter fed predominately on solid food when approximately 48 days old.

The weights of the six smallest juveniles taken by live trapping in June and July ranged from 83.0 to 97.2 gms, and their estimated ages varied from 9 to 11 weeks, averaging about 10. All were observed foraging and feeding independently and were probably completely weaned. The seven smallest juveniles killed weighed from 79.6 to 109.8 gms and were 9 to 11 weeks of age. Their stomachs contained solid foods with no trace of milk.

Older young may sporadically attempt to nurse. One of a litter of five juveniles about seven or eight weeks old observed near their den tree on May 22, 1951 was seen to make a desultory attempt to suckle the parent. At the time the young were feeding primarily on silver maple samaras. Two juveniles about 11 weeks of age were seen attempting to nurse a female on June 13, 1952.

Age at Leaving the Nest and Dispersal. Judging from the behavior of captive litters, the young probably explore the nesting cavity as soon as their eyes are open. They apparently make limited excursions from the nest when about six or seven weeks old but probably do not forage any distance from the home site until about 10 weeks of age. Five young

of a litter about six weeks old were captured over a period of several days as they fell to the ground, one by one, while exploring the entrance to their nest cavity in the outside wall of a house. Individuals of the youngest litter observed outside a nest were about seven weeks of age. Their activity was confined mostly to the den tree and two nearby trees. They seldom ventured to the ground and then appeared loath to move more than a few feet from the base of the tree. For a period of several weeks after venturing from the nest the young squirrels are quite tame and unwary.

As they grow older the juveniles extend their range of movements, but the litters tend to remain together in a more or less circumscribed area near the home site until the young are about 12 or 13 weeks of age. At night they retire to the original den or to a nearby one. On the 47 acre lower campus study area the young of six litters were usually observed within a short distance of their respective nest sites until June 23, when they were about three months old. A week later the families were less distinctly segregated and by July 4 the litters had dispersed and the young were scattered widely over the area. Live trapping studies on this area suggest that most of the spring juveniles disperse between late summer and the following June. Of 15 juveniles marked in June and July 1952, only one remained on the area the following year. The majority of the spring juveniles probably emigrate in the fall. No data is available on the movements of summer juveniles from this area.

Parental Care. Observation indicates that there may be a somewhat loose association between the adult female and her young for a few weeks following the weaning period, which in the case of most spring litters does not usually extend beyond the end of June. From May 22 to June 4, 1951 observations were made on five young about seven weeks old who were attended by two females. The nipples of both adults indicated that they were lactating or had recently nursed. Both were solicitous of the welfare of the young. On one occasion they joined a juvenile who had strayed to a nearby tree and by their combined efforts succeeded in getting it to follow them and led it across a street to the den tree. While they sat side by side in a Norway maple one evening, one adult female mounted the other and appeared to comb its fur with quick nibbling bites and rapid strokes of her fore feet. A few moments later the other reciprocated in a similar manner. They occasionally touched noses and gently nudged each other about the flanks. If one moved off the other soon followed. There seems to be no ready explanation for this relationship between two nursing or recently lactating females and what was apparently only a single litter, judging from the uniform size and appearance of the young. It is possible that one of the adults had lost its own litter and was tolerated by the other.

On June 1, 1952 an adult female feeding in the same tree with 7 to 8 week old young was seen to

drive off an approaching adult when the latter was still 50 ft. away. Other instances of a female associated with partly grown young were noted on June 12, 1953 and June 13, 1952. On the latter date the young attempted to suckle the parent. A female who was striving to induce two juveniles to follow her up a tree was noted June 18, 1952. When the young wandered away she would pursue and cut them off. An adult female and a juvenile male about 13 weeks old, who might have been her offspring, were seen feeding and foraging together on June 24, 1953. No evidence of adult males participating in the care of the young was obtained.

As noted previously, on February 3 and March 26, 1952, a pair of adult and immature females were shot from the same nest, indicating perhaps that at least one of the litter had remained with the parent over winter. Allen (1943) has cited instances of associations of this nature in fox squirrels.

NESTS

In the Ithaca region, leaf nests, tree cavities, fallen trees, rock piles, underground burrows, and man-made structures provide red squirrel nesting facilities. Leaf nests were constructed in white pine, red pine, hemlock, larch, red maple, sugar maple, blue beech, bitternut hickory, white ash, beech, black cherry, red oak, and white oak. There was apparently no preference for a particular tree species as long as it fulfilled other requirements of a nesting site. Trees containing nests were from 4 to 16 in. in diameter and from 15 to 70 ft. high. Nests were built from 12 to 60 ft. above ground. Mayfield (1948) has found a typical outside nest containing young on the ground at the base of a small tree.

Nests were placed either adjacent to the trunk or farther out on limbs that offered sufficient support and were fashioned from a considerable variety of plant materials. Availability dictates in large measure the kind of material to be used, although a predilection is shown for grape bark, when available, as a lining material. Occasionally an old hawk or crow nest served as a foundation for a nest. Many nests were placed in a clump of grape vines and a few were entirely suspended within these tangles. A number of outside nests found in hardwoods or mixed hardwood-conifers were composed of three fairly distinct layers. Within a shell of loosely interwoven twigs with leaves attached is a compact intermediate layer of compressed leaves. In some cases the outer covering does not extend over the top of the nest, thus leaving the second layer exposed above. The innermost layer is a well-consolidated, roughly spherical mass of finer plant material enclosing a chamber about 4 to 6 in. in diameter. The nest chamber is lined with dried grasses, soft inner bark or other fibers, and bits of moss, feathers, fur, or shreds of paper. Access to the chamber is by one or two entrances at the side of the nest. Below the chamber, at the juncture of the inner nest and middle layer, is usually

a sodden, decomposing area that results from drainage.

The average diameter and depth of four nests in use were 12.5 in. (12-14) and 15.0 in. (8-19), respectively. The average diameter of gray squirrel nests in the Ithaca area is 18 in. (Roecker 1950), hence the smaller size of red squirrel nests usually distinguishes them from those of the former species although there is some overlap. It is probable that the nests of either species are utilized by the other since a gray squirrel was once flushed from a nest in which two red squirrels had been killed a week previously. Seton (1909) also mentions a case of a gray squirrel occupying a red squirrel nest box. Deer mice also occasionally inhabited old red squirrel nests.

Temporary or summer nests are also constructed. One examined in June was located within a maze of branches where the crown of a felled hemlock had caught in the upper branches of a red oak. It was formed of a loose shell of green oak and basswood twigs and leaves that had been cut from nearby branches and a more compact inner lining of leaves. There was no inner nest of finer material. It measured 18 in. in diameter and 12 in. in depth.

Cavities in trees were more intensively utilized in the various habitats studied than were outside nests. No preference was noted between woodpecker or natural holes nor between living or dead trees. The characteristics of cavity, entrance, and site are undoubtedly of greater importance than the tree species in determining red squirrel utilization. Dens were observed in the following trees: white pine, hemlock, black cherry, apple, ailanthus, silver maple, sugar maple, red maple, butternut, shagbark hickory, pignut hickory, beech, red oak, black oak, white oak, and white ash. The diameters of these den trees varied from 12 to 36 in. and their height from 20 to 60 ft. Den entrances were from 7 to 50 ft. above ground. Active dens in live trees often had fresh gnawing visible around the entrance. This is apparently done by the animals to arrest the growth of scar tissue and maintain the den opening at a constant size (Baumgartner 1939). Allen (1942) and Brown & Yeager (1945) have stressed the protective value of cavity nests with respect to fox and gray squirrels. The relatively greater sense of security that red squirrels seem to feel in tree dens is evidenced by the ease with which they are dislodged from leaf nests as contrasted to the oftentimes impossibility of flushing them from a den tree.

During the colder months several community den trees were found in which three or four squirrels lived in harmony. In one instance, it appeared that a red and gray squirrel inhabited separate holes in the same tree.

Underground nests were noted in all types of habitats but were encountered most in hedgerows, particularly in winter. Many of the underground burrows were located beneath old stumps and were conspicuous by the litter of food remains near their entrances. Hatt (1929) has described the configura-

tion of several underground nests excavated in northern New York.

Nests were also found in a stack of fence rails; on the rafters or between the partitions of city dwellings, cabins, and farm buildings; in a pump shaft housing of an unused windmill; bird houses; rock piles; and a fallen tree. It was reported to me by William Barth that nests containing young are often discovered in the spring by beekeepers when they unpack their hives from old wooden crates in which they are stored over winter. These storage boxes measure 4 x 4 x 4 ft. and hold four hives packed with shavings. The boxes are placed in sheltered situations, conifer plantations being preferred. Red squirrels gnaw through the sides and construct their nests with materials transported from outside. The nests are invariably placed against the side of a hive, perhaps to secure the heat produced through the respiration of the bees within. The top of the nest is said never to be below the level of the packing material. Weasels, raccoons, and mice also utilize the boxes for nesting sites but gray squirrels have not been reported using them.

Non-parasitic arthropods collected from five nests included the centipedes *Lithobius forficatus* and *Geophilus rubens*; beetles of the families Chrysomelidae (*Haltica chalybea*), Staphylinidae (*Aleochara* sp. and *Oxyptoda* sp.), and Lathridiidae (*Costicaria serrata*); Lepidoptera larvae of the families Noctuidae (*Epizeuxis acmela* and *E. americanis*) and Pyralidae; the spiders *Coriarachne versicolor*, *Xysticus punctatus*, and *Pityohyphantes costatus*; and the pseudoscorpion *Chelifer cancrroides*. Specimens of unidentified chalcid wasps and Collembola were also obtained. Various amounts of detritus including hairs, fecal pellets, nut shells, and insect remains were found within most nest chambers. Seton (1909) lists the contents of two nests that were carefully analyzed.

MOVEMENTS

Calculation of Home Range. Burt (1943) has defined home range "... as that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." Studies have shown that the size of the home range may be influenced by age, sex, season, population density, habitat, and other factors. The majority of small mammal home ranges have been studied by plotting points of capture in live traps set in a grid pattern and then connecting the outlying points with straight lines, or with curved lines that exclude areas not utilized by the individual. Often a boundary strip equal to half the distance to the next trap is added to the minimum limits of the range to compensate for the absence of traps in the intervening area. Chitty (1937), Mohr (1947), and Hayne (1949, 1950) have discussed the ways in which trapping techniques, number of traps, size of grid, and method of calculation may affect the size of the trap-revealed home range and considerably complicate the relation between it and the animal's true home range.

In order to circumvent drawbacks of the grid

trapping method, the technique employed in the present study involved the use of only a small number of traps. These were set more or less at random through the habitat in sites likely to be visited by squirrels. They were frequently shifted so as to adequately sample the entire area. Although specific comparisons were not made, field experience indicated that this system would yield more satisfactory results than a grid trapping procedure in that the traps would probably interfere to a lesser extent with the normal activities of the animals and yet take a greater proportion of the individuals resident on the area. In regard to the latter, Evans (1951) has observed that grid trapping may be satisfactory for some species but in others its advantages may be nullified by an inadequate sample. In one area, trapping data were largely supplanted by direct observations of marked animals, as has been done by Ingles (1947) and Yerger (1953) for other sciurids. The configuration and area of the home range was determined by connecting the extreme points of capture or observation with straight lines according to the "minimum home range" method of Mohr (1947). It is believed that this index of the true home range gives the most comparative and conservative results. It departs less from the observed facts than do those methods that add a boundary strip to the line connecting outside points of capture or consider the greatest distance between points of capture as being the diameter of a circle or the long axis of an ellipse which, in turn, represents the home range (Hayne 1949). In addition, this method is the most convenient to apply with data obtained from irregular trap settings and random observation.

Size of Home Range. No systematic studies of home range in the red squirrel have apparently been conducted. Available data on this aspect of the life history are largely estimates based on observations at different seasons and for varying periods of time. However, they serve to illustrate that considerable variation is to be expected in the size of the home range in different environmental situations and in various parts of the species' range.

Seton (1909, 1929) estimated the average home range size to be between 6 and 10 acres. Klugh (1927) considered it to be an area of about 250 yds. square. Hatt (1929) watched a pair for about three months and concluded that their greatest range of activity was about 200 yds. in diameter. Hamilton (1939) considered an acre of territory sufficient where food was abundant. He records six squirrels occurring in a three acre woodlot. On the Cornell University campus he found that individuals inhabiting a half acre oak grove seldom ventured more than a few rods from the trees.

In this study, 105 red squirrels were live trapped, marked for permanent and visual recognition, and released on three areas located within the confines of the Cornell University campus. Sufficient data were accumulated to calculate 43 home ranges.

Intensive observations on the movements of squirrels residing on a 47 acre portion of the lower campus

were made from June 1 to July 7, 1952 and from June 22 to August 9, 1953. This area has a park-like aspect of widely spaced buildings, spacious lawns, and numerous large trees. The predominate tree species include American elm, white oak, red oak, Norway spruce, Douglas fir, larch, pignut hickory, sugar maple, silver maple, Norway maple, catalpa, and horse chestnut. Fifteen or fewer live traps were employed to capture as many individuals as possible in the shortest time while adequately sampling the entire area. The traps were set between 10 and 11 p.m. and were usually taken up the following morning before 9. In this way the population was probably not greatly influenced by the trapping activities. Observations of marked individuals with 6 x 30 or 7 x 50 binoculars provided the major share of information relating to movements. The method used was that of moving slowly but steadily in a circuitous route covering all parts of the study area and recording the position, observed movements, and activity of the marked animals as they were encountered, but not concentrating upon any one individual for more than several minutes. More detailed information on individual movements might have been obtained by following single squirrels for as long as possible, but fewer home ranges could have been studied in the same amount of time. Observations were made almost daily from sunrise until sometime between 7:30 and 9 a.m. and often again in the early evening until dusk. At these times the squirrels were most active and human activity on the campus was least.

Twenty-nine squirrels were captured and marked in 1952 and 38 in 1953. The 67 individuals were trapped or observed a total of 529 times. Home ranges were calculated for 37 individuals captured or observed five or more times and are given in Table 13. The greatest distance between points of capture

TABLE 13. Size of home ranges of 37 adult and juvenile red squirrels from June 1 to July 7, 1952 and June 22 to August 9, 1953 on the 47 acre lower campus study area.

Age	Sex	Number	Average Number of Captures and Observations	Mean Home Range in Acres	Extreme Home Ranges in Acres
Adult	M	6	9.2	6.03 ± 1.51	0.47-10.76
Adult	F	7	14.7	4.72 ± 1.48	1.00-11.13
Juvenile	M	18	8.9	2.73 ± 0.67	0.06-7.04
Juvenile	F	6	23.2	5.90 ± 0.31	2.14-8.23

or observation was measured for each home range. This distance averaged 908 ft. (270-1310) for adult males, 691 ft. (500-1220) for adult females, 633 ft. (125-1170) for juvenile males, and 802 ft. (390-900) for juvenile females. The variation in the area of the home range within each sex and age class is considerable. Although adult males may actually have a slightly larger average home range than adult females the differences in the present data are not statistically significant. All adult females whose home ranges were studied were in a post lactation condi-

tion. It is possible that their movements are somewhat more restricted when they are caring for young earlier in the season.

The home ranges of adults averaged slightly larger than those of juveniles, 5.32 acres as compared to 3.52 acres, but again these differences are not highly significant in view of the variability within each class. Juveniles shortly after leaving the nest have a range of activity rather closely restricted to the vicinity of the natal den tree, but it expands rapidly as they begin to forage more extensively.

The areas and greatest dimensions of the home ranges used by adults of both sexes were noticeably smaller in 1952 than in 1953. In 1952 four males had a mean home range of 4.36 acres; the greatest dimensions averaged 761 ft. The home range of two individuals in 1953 averaged 9.36 acres in area and 1200 ft. in greatest dimension. Home range averaged 2.58 acres for three females in 1952 and 6.31 acres for four individuals in 1953. The longest distance recorded between captures or observations averaged 587 ft. in 1952 and 770 ft. the following year. The differences between the two years were not pronounced in juveniles. The mean home range of nine individuals in 1952 was 3.78 acres, the average greatest dimension being 541 ft. In 1953 the home range of 15 juveniles averaged 3.36 acres and the mean distance between extreme captures or observations was 756 ft. An explanation was offered by a variation in the food supply. In 1953 fallen American elm seeds, an important food on this area, were less abundant than during the earlier period the previous year, and it appeared that the squirrels were forced to forage more extensively to utilize more localized food sources as they became available.

Several home ranges were calculated solely from trapping records in a heavily wooded 10.3 acre section bordering the Cascadilla gorge at the southern edge of the university campus. Large hemlocks dominate the more mesic steeper slopes of this gorge, whereas a second growth hardwood association prevails on the drier, level ground along the northern border of the area. Red squirrels were most active in the conifers and were less commonly seen foraging in the drier hardwoods than were gray squirrels and chipmunks. The fact that the woodlot was only about 500 ft. wide throughout its length did not appear to have any limiting effect on squirrel movements.

The system of live trapping probably had little or no effect on the normal movements of the animals. Traps, which never exceeded 12 in number, were usually placed in lines following the contours and spaced from 50 to 200 ft. apart. They were shifted at each trapping period so that the whole area was well sampled. Trapping periods were seldom longer than 10 days and were separated by intervals varying from about two weeks to four months.

Home ranges of six adults captured four or more times during the 20 months period from January 1951 to August 1952 averaged $0.36 \pm .08$ acres. The greatest distance between points of capture averaged 308 ft. The mean home range of two females (0.44

acres) slightly exceeded that of four males (0.32 acres). The greatest dimension of the female ranges averaged 325 ft., that of the male ranges, 300 ft. The significantly smaller home range of the squirrels in this area are probably due in large measure to the greater density of food and cover than obtain on the much more open lower campus area.

In both study areas the home ranges of males and females and adults and juveniles overlapped each other to a varying extent. When individual ranges were plotted on maps there appeared to be no tendency for either sex or age group to occupy mutually exclusive areas. An example of the degree to which range overlap occurred is that of a small (.47 acre) home range of an adult male which was encroached upon by those of five other adult males, an adult female, and five juveniles. On the lower campus, two females in 1953 occupied home ranges that overlapped almost completely, corresponding closely in area and outline. Among juveniles there was a slight tendency for the home ranges of members of the same litter to be somewhat separated from those of other litters, but this was almost certainly due to the inclination of the young squirrels to remain in the vicinity of the nest site rather than an expression of any inter-litter antagonism.

Shifting Home Ranges. Of the 100 squirrels marked and released on the lower campus and Cascadilla gorge areas, 77 were subsequently retaken. The highest percentage of animals retrapped were taken within a short time of the original capture, the proportion of marked to unmarked individuals in the population becoming less over longer periods (see populations). Natural mortality, accidental death, predation, and dispersal of juveniles undoubtedly account for much of the observed population turnover. Certain individuals may continue to reside on the area but somehow escape capture after one or two times. Linduska (1950) has suggested that some individuals which fail to be retaken after the initial capture may be transients with no fixed home area. He recorded one juvenile female 5.5 miles from the study area in which it was first captured. Such an instance may be that of an adult male trapped and released on the Cascadilla area March 6, 1951 and shot 1.2 miles upstream from the place of capture on October 31, 1951.

An additional factor in population turnover on an area seems to be a gradual shifting of some home ranges until they may no longer be included nor extend within the trapping perimeter. One specific instance of such a shift was recorded. On the lower campus, a parous yearling female was marked as a juvenile in 1952. The following year she occupied a home range about 700 ft. removed from the nearest boundary of the previous year's range. The home area in 1953 comprised 8.55 acres as compared with 6.81 acres in 1952. Circumstantial evidence of a shift in the home range of an adult male was obtained by plotting the direction taken and the den site sought each time the animal was released from a trap. The individual was captured six times in

January and February. When taken in April its release patterns had changed to a new direction and converged on a different den tree, approximately 500 ft. from the one utilized earlier. Linduska (1950) found that about 46% of the individuals on his study areas shifted their residences between woodlots or other habitats.

Evidence obtained on the lower campus area in 1953 indicated that a particular food source may influence the shape and size of the home range and might even induce some individuals to actually shift their home range. The home ranges of an adult male and female and five juveniles were distorted from 600 to 900 ft. beyond the cluster of points which marked their normal foraging range by observations of them feeding in a small mulberry at the periphery of the study area. Three of the five juveniles were not seen again in their former haunts after being observed at this site. Whether such isolated occurrences of an individual so far removed from its habitual foraging area are to be considered in the nature of an occasional movement beyond the limit of the actual home range and not to be included in the calculation of the latter (Allen 1943) or else assumed to be a part of the home range seldom visited until attracted by a newly available food is difficult to determine. To attempt to draw the line between observations which are considered to represent the normal home range and those representing occasional forays beyond the usual limits seems to introduce an additional subjective element into the calculated home range, which is already only a crude abstraction of the actual pattern of the animal's movements.

Permanency of Home Ranges. Ten of the 100 squirrels marked on two study areas apparently occupied the same home range for periods varying from 12 to 27 months, with a mean of 20.8 months (Table 14). An animal was considered to be within the confines of its original home range when the distances between subsequent captures or observations and the original capture were less than the mean greatest dimension of the home range of the same sex and age class in that particular area. Although the data are meager, it might be inferred that the greater number of females with permanent or semi-permanent home ranges and their longer average occupancy of these areas (22.3 months as compared with 15.5 months for males) is an indication that they tend to be more sedentary than males.

Homing. That red squirrels apparently possess some sort of homing ability was demonstrated by Hamilton (1939) by marking and liberating squirrels who returned to their home areas from distances of 3/4 and 1 mile. Some additional evidence pertaining to the homing behavior of the species was obtained in this study, but it was largely incidental to other phases of the work.

Five adults and four juveniles were released at distances ranging from 1400 to 3100 ft. from the place of capture or center of the known home range. Two adult females who had resided on the Cascadilla area for over a year were released 1600 ft.

TABLE 14. Dates and distances of subsequent recaptures from the point of original capture of squirrels considered to occupy the same home range over periods of a year or longer.

Sex	Date of Original Capture	Dates of Subsequent Recaptures and Distance (in feet) from Original Capture Site	
F.....	Jan. 4, 1951	Apr. 7, 1952 (60)	Mar. 14, 1953 (500)
F.....	Jan. 5, 1951	Aug. 15, 1952 (80)	
F.....	Jan. 28, 1951	Aug. 9, 1952 (80)	
F.....	Jan. 31, 1951	Apr. 2, 1952 (70)	Mar. 31, 1953 (150)
M.....	Feb. 7, 1951	Mar. 31, 1952 (150)	
F.....	Feb. 9, 1951	Apr. 4, 1952 (200)	
M.....	Mar. 6, 1951	Nov. 30, 1952 (150)	
F.....	Mar. 16, 1951	Apr. 6, 1952 (200)	Mar. 13, 1953 (270)
F.....	June 11, 1952	May 28, 1953 (150)	
M.....	June 14, 1952	June 23, 1953 (800)	
M.....	June 14, 1952	July 4, 1953 (380)	

from their home sites on August 9 and 13, 1952. One was retrapped in its home area two days later but failed to be retaken when released 2400 ft. away. The other was not recaptured. An adult male, resident on the area 21 months, returned to its established quarters from a distance of 1600 ft. between August 8 and November 28, 1952. When liberated at 3000 ft. it was not retrapped. Another adult male captured for the first time August 8, 1952 was retaken on November 28 near the original site, 2300 ft. from the point at which it was released. It did not reappear in subsequent trapping periods following a second liberation at 3100 ft. A subadult and adult taken on the area November 29, 1952 were not recovered following release at 3000 ft. It should be noted that some of the animals failing to be retaken in their home areas following the initial or second release may actually have returned and yet escaped subsequent capture due to the small number of traps employed and the irregular trapping periods.

On the lower campus, four juveniles whose home ranges had previously been determined were re-trapped during early July and released 1400 to 2500 ft. distant in unfamiliar territory. A female released 1400 ft. away at 7:25 a.m. was back in her usual haunts 12 hours later. When removed 2500 ft. on July 11 she failed to return, apparently settling in her new surroundings since she was killed less than 200 ft. from the release point on September 29.

On July 3, 1953 a male was liberated 1700 ft. from the nearest boundary of his home range. His subsequent movements were carefully followed and seemed to indicate a definite homing sense rather than a random searching for familiar territory. Since the trees were widely scattered on the area he had to cross, most of his progress was on the ground from the base of one tree to that of the next. He was hesitant to negotiate open areas more than 50 ft. wide yet was seen to make one dash of 135 ft. to another tree. He sometimes made several false starts before proceeding to the next tree and occasionally went up into the lower limbs and out to the tips of the branches in several directions as if to orient himself. The squirrel moved consistently in the direction of its home region and followed a rather direct course,

deviating only to take refuge in an occasional tree somewhat removed from the route. Within an hour he had returned 700 ft. of the distance to the home site and there established himself. The limits of his new home range as determined from six observations made the following week were 500 to 600 ft. from the nearest boundary of the former range.

Another juvenile male returned to its established range from 1800 ft. away within two days of its release on July 4, 1953. A third juvenile male failed to return from a similar distance.

TERRITORIALITY

Territory has been defined by Noble (1939) as "... any defended area." Burt (1943, 1949) has clarified the concepts of territoriality and its biological implications in mammals, recognizing the existence of two fundamental types concerned respectively with food and shelter and breeding and care of young. On the basis of examples afforded by numerous species of birds and two mammals, Darling (1952) concluded that territoriality is essentially a social phenomenon, reflecting an inherent tendency for individuals of like species to congregate and be in contact. He considered that the so-called fighting or aggressive acts occurring at the peripheries of territories, in the areas of contact, were in many instances probably only a type of formalized display that is beneficial and mutually stimulating to the individuals involved.

Territorial behavior is properly studied by direct observation of animals under natural conditions. Home ranges calculated solely from trapping records afford presumptive evidence that territorial defense exists if they are mutually exclusive. It cannot be inferred from overlapping ranges that territoriality is non-existent since trapping may influence an individual's ability to defend its territory by modifying its psychological or physiological reactions in addition to merely restricting its activity over various periods. This criticism is largely invalid when home ranges are derived from observations of marked animals that are captured as infrequently as possible. Differences in the level of territorial expression within a species may be related to age, sex, season, or social factors.

Walton (1903), Seton (1909), Klugh (1927), Hatt (1929), Gordon (1936), and Clarke (1939) have reported instances of territorial defense in red squirrels. The conclusion reached in the present study is that red squirrels do not normally establish exclusive property rights over specific areas within the home range, and that territorial behavior is usually restricted to a small area immediately surrounding a feeding station or particular den site over which an individual holds priority by being first to occupy it. Circumstantial evidence from trapping supports this view since individuals of either sex and any age group were frequently taken in the same trap within a short interval. Home ranges as calculated overlapped broadly, with no suggestion of a tendency to be mutually exclusive. Field observations further

discouraged the idea that individuals consistently defended any specific or appreciable amount of area within their home range.

Much of the scolding, squabbling, and chasing that was observed was considered to be primarily of a social nature and not actually aggressive. This type of behavior has been shown (see activity) to reach daily peaks in the hours shortly after sunrise and before sunset; seasonally, it seems most intense in October and November. Instances construed to be actual defense of territory were relatively infrequent in proportion to the number of hours of observation. In most cases such acts were limited to an utterance of the harsh extreme anger note, or a short offensive lunge, when another squirrel approached too closely to a feeding individual. These exchanges took place between both sexes and juveniles and adults. Another squirrel could often approach within a foot of a feeding individual before an antagonistic response was elicited. Although young exhibit territorial reactions at about seven weeks of age, they incline to be somewhat less territorial than adults for sometime after leaving the nest. Two juvenile males about 14 weeks old were captured simultaneously in the same trap on July 1, 1953, indicating that they may have been feeding in very close proximity prior to capture. It was occasionally noted that a feeding squirrel when approached by another would begin to eat voraciously, at the same time attempting to sound the warning note. This behavior was frequently observed among captives.

Occasionally a more extensive chase was given, but it did not always result in effective exclusion of the encroaching individual. On April 27, 1951 an adult was feeding at the base of a tree when another squirrel crossed over into the same tree and descended to the ground. It passed within three feet of the first individual who presently gave chase. They were lost to view about 200 ft. away but could be heard scolding. Within a few moments the original animal returned by way of the tree tops, descended, and resumed feeding. On June 14, 1952 an adult female was seen to chase off another who approached her as she fed on the ground. The latter soon returned, and the two foraged amicably on either side of a tree. Both were animals who had borne spring litters. An adult male was observed July 7, 1952 in vigorous pursuit of another adult who seemed determined to get into the same tree. Each time the interloper reached the tree the male would give the anger note and chase it spirally up and down the trunk. Once they actually engaged in combat on the ground for a few moments. The invader was persistent and did not seem cowed by the defending male in whose home range the disputed area lay. It was observed pursuing the latter a short time later in the same vicinity.

Several other cases were recorded in which an individual was unable to successfully defend its feeding area. On June 27, 1953 a juvenile male, feeding on shelled corn at the base of a tree, attempted to drive away another young male who was trying to reach

this food. Although the first animal scolded harshly and chased the intruder several times, the latter eventually succeeded in reaching the food. On January 28, 1951 an adult male routed an adult female from her feeding station, even though she scolded harshly and assumed a defensive posture at his approach. Three weeks earlier he had been seen to charge an unmarked adult feeding at the base of the same tree, fight with it on the ground, and chase it about 200 ft. away. One might infer from this that specific feeding areas are defended within the home range. However, this squirrel was observed feeding in the same location with two others, including the female mentioned above, on numerous other occasions without displaying any animosity.

Females with nest young probably exercise a greater effort to defend a territory around the nest site, but only a single incident of this nature was recorded. On June 1, 1952 an adult female with enlarged nipples who was associated with three young about seven to eight weeks of age was seen to pursue and drive away an approaching individual (possibly a male) when it was still at least 50 ft. away.

On November 28, 1952 an adult male was released for a homing test in an area unfamiliar to it on the lower campus. As it descended from a tree in which it had taken refuge it was seen by a resident red squirrel foraging nearby. The released animal retreated back into the tree as the other squirrel moved toward it. The latter ascended the tree, sniffed among the branches, gave the anger note and long "churr" call, and proceeded to drive the other individual from the tree. It chased the newcomer about 90 ft. then returned to the tree in a high state of agitation, giving the long calls at frequent intervals. This observation suggests that some of the weak territorial expression that seems to occur between certain individuals is perhaps due to the fact that animals living on a given area may be somewhat tolerant of their neighbors but immediately recognize the presence of a stranger and attempt to exclude it from the vicinity. Nice (1939) has demonstrated that song sparrows on their nesting grounds are personally acquainted with their neighbors within a radius of 100 m. Studies of this nature among small mammals might be profitably conducted.

Occasional altercations between two or three squirrels over a nest cavity were observed. It appeared that the first animal to enter the hole was able to defend it successfully. On July 5, 1952 two adults were seen attempting to enter a cavity in a sugar maple being defended from within by a third squirrel. Despite considerable high pitched squalling and scrambling the two outside were unable to force entrance or drive out the third. Two individuals were seen fighting over a hole on November 2, 1952. When the occupant of the cavity tried to leave it the other would drive it back and thrust its head and shoulders into the entrance, only to recoil suddenly as if bitten. If it withdrew from the entrance the squirrel within would poke out its head and scold shrilly.

Captive individuals would initially attempt to defend their nest boxes from newly introduced individuals, but would usually share them within a few days. On February 9, 1951 a newly trapped female was placed in a large outdoor cage occupied for some time by a lone adult male. A chase ensued in which the male relentlessly drove the female about the cage. It ended with the latter sitting on top of the nest box. When she began to "chirp" the male flew at her and drove her down behind the box. He entered the box but dashed out immediately and went down to the floor of the cage to feed, all the while uttering the anger cry. When the female moved toward the entrance he rushed at her again, but she entered the box and successfully repulsed his efforts to drive her out. It was several days before he could again gain access to the nest box.

General observation provided an impression of the possible social implications of territorial behavior in the life history of the red squirrel. A rather marked gregarious tendency was often noted, in which individuals occupying a given area tended to be bunched together rather than being more uniformly dispersed. In some instances this could be attributed to attraction to a more favored niche within the habitat, such as a clump of hemlocks in a hardwood stand; but the phenomenon was also observed in regions of apparently homogeneous environment. Where such concentrations of individuals occurred, social expression in the form of increased vocalization and chasing seemed disproportionately greater than when densities were less. Increased territorial expression within these aggregations may have promoted a higher level of excitation among the individuals than would be the case were they dispersed more regularly throughout the habitat. Such a phenomenon may produce an intensification of feeding and reproductive activity.

Contrary to the prevailing notion, no conclusive evidence was obtained to indicate that there exists any marked antagonism between the red and gray squirrel. Occasionally, red squirrels were observed in pursuit of grays, who not infrequently would promptly return to the same area once the red gave up the chase and not be further molested. At other times feeding gray squirrels were seen to successfully drive off inquisitive red squirrels, although they did not press their attacks as intensely as did the latter.

On the lower campus study area, where ample opportunity was had to study the relations between red and gray squirrels and chipmunks, there appeared to be no marked intolerance between the three sciurids. There was some difference in their respective feeding habits that may have somewhat reduced the number of contacts between them, but this factor was certainly of a very minor nature. Grays fed most boldly, often foraging out to the center of the most open areas. The red squirrels were more inclined to remain in closer proximity to the trees. They often appeared nervous and hesitant when forced to cross an open area. Chipmunks were by far the most circumspect in their foraging activi-

ties. Seldom did they venture from the protection of shrubs, bases of trees, or sides of buildings. On unnumbered occasions red squirrels and grays fed within a few feet of one another on the ground or in the trees without any sign of animosity. Their relations with chipmunks were similar. It is probably safe to state that intraspecific strife was more common than antagonistic behavior between the species.

In many habitats in which red squirrels were hunted, densities of gray squirrels were equal or higher. The two species often foraged and fed on the same area. Here, too, the grays made considerably longer foraging excursions than did the red squirrels. The nature of any competition between them on these areas was probably indirect, being associated with their similar dietary and nest requirements. In some places a tendency was noted for the two species to be somewhat segregated, but this was apparently only a response to ecological factors.

DEFORMITIES

Loss of a portion of the tail was the commonest deformity recorded. Of 247 adults examined, 20.2% had sustained injury to the tail, involving from a few joints to nearly half. The stub-tailed condition was recorded for 25.0% of 140 adult males and 14.0% of 107 adult females. Only 7.7% of 156 immature specimens had damaged tails. Most of the latter exhibiting this condition were older animals collected in the late winter or early spring. Seton (1909) noted that about half of the squirrels he collected about Kenora, Manitoba had some tail injury. Four out of 42 specimens (19 were adults) taken by Hatt (1929) in northern New York and Massachusetts had a portion of the tail missing. All were adults. Grimm & Whitebread (1952) found the occurrence of bob-tailed adults rather high in areas of northeastern Pennsylvania. It is generally assumed that the loss occurs mainly during chases between individuals and at the time of rutting. This might be reflected in the higher frequency of the injury among adult animals. The present data suggest that there may be more fighting and chasing between adult males than females.

The skin and hair of the tail tip strip off easily, leaving the vertebrae exposed. An adult male collected July 6, 1953 had the terminal inch of the tail missing, but the dried exposed vertebrae had not yet been lost. Often an abnormal swelling occurs at the tip of the damaged tail. In several instances, when the caudal vertebrae were cleaned and examined, the vertebra at the point of the break showed traces of injury. The shortest stub tail noted was that of a subadult female. It measured 72 mm. An adult male and female had tails only 73 mm and 76 mm long. The average tail length is 124.3 mm. Bob-tailed individuals are not visibly handicapped by the shorter length of this member.

Other abnormalities were rare. One adult had the distal phalanx of a front digit lacking. Another had two claws on the left fore foot missing. John G.

New told me of a red squirrel taken in a steel trap whose right fore leg had to be amputated at the elbow. The loss of the limb did not noticeably interfere with the animal's agility and it was subsequently released.

Few skeletal defects were noted. Two slight cases of malocclusion were recorded. In both, the lower incisors had worn the tips of the upper incisors into a v-shaped notch instead of the normal chisel-shape. One of the specimens had been a wild individual in good condition when collected; the other was a captive that seemed to experience no difficulty in feeding. The acromion process of the left scapula of an adult female was deformed and much roughened in appearance, possibly due to breakage or an arthritic condition. The right innominate of an adult male was abnormally swollen and malformed in the acetabular region. The right femur of a subadult male was slightly crooked and swollen in the middle of the shaft. It apparently had been fractured and healed. These defects had not been noted to interfere with the activity of the individuals prior to collecting.

LONGEVITY AND MORTALITY

Longevity. Klugh (1927) reports a captive red squirrel that lived nine years. Following its fifth or sixth year it began to show signs of decreased agility. A wild individual was apparently observed by Walton (1903) over a period of ten years. Linduska (1950) had records of several squirrels known to have lived over two years. A single adult male was at least three years old when last handled.

Since the present study was of relatively short duration, adequate knowledge of the life span of individuals under natural conditions was not obtained. Thirteen squirrels were known to have had a minimum age exceeding 16 months. Five were between 18 and 22 months. Three were at least two years old when last handled. Three others were at least 27, 31, and 31 months, respectively, when last trapped. An adult female approaching the breeding condition for the second time of the season was considered to be at least 22 months old when collected June 11, 1952, since it is not likely that yearling females breed twice in their first season (see fecundity). This individual was killed May 28, 1953 at an estimated age of 33 months.

Mortality. Predation does not appear to be a significant factor in red squirrel mortality. Hatt (1929) presents a detailed account of the enemies of the red squirrel. Only one predator kill was observed during the course of this study. The appearance of the remains indicated the work of a hawk or owl. Cats and dogs were observed stalking red squirrels on the lower campus area but were never seen to capture one. Road kills account for some mortality. Of 440 specimens obtained by all methods for autopsy, 22, or 5%, were highway victims. Others were seen, but were too badly damaged to collect. Young squirrels within a month or two of leaving the nest are more frequently victims than adults.

PARASITES

Endoparasites. Squirrel carcasses were not systematically examined for internal parasites. An adult male live trapped July 13, 1952 was killed and found to have a high infestation of an intestinal flagellate (*Trichomonas*) and a coccidian (*Eimeria*). The latter was particularly abundant. The entire small intestine was congested with all stages of the life cycle. No effects of this particularly heavy infection were revealed in the animal's behavior before death. Two cysticerci of an undetermined cestode were noted in the lobes of the liver of an animal killed August 4, 1952. Studies by Rausch & Tiner (1948) and Tiner & Rausch (1949) suggest that red squirrels are not as subject to infection with parasitic helminths as are fox and gray squirrels.

Ectoparasites. Mites (Acarina). Six species of parasitic mites and three specimens of non-parasitic forms (Oribatei) were collected from 31 squirrels and three nests. The oribatid mites were taken on the squirrels.

Euhaemogamasus ambulans Keegan. 131 collected (6 males, 125 females). An additional 29 females were secured from a nest.

Euhaemogamasus liponyssioides (Ewing). 1 female collected.

Haemolaelaps glasgowi (Ewing). 41 collected (1 male, 29 females, 11 unsexed).

Haemolaelaps megaventralis (Strandtmann). 3 females collected.

Amblyseius grandis Berlese. 1 female collected.

Dermanyssus gallinae (Linnaeus). 4 females collected from a nest built in a windmill next to an abandoned poultry yard.

Three squirrels had thick scab-like encrustations on their bodies. These areas were restricted to the ears, feet, tail, and caudal end of the scrotum. They were apparently caused by a "scab mite" (Sarcoptidae) of undetermined genus. The affliction seemed to have no deleterious effects on the animal. A single chigger, *Euschöngastia setosa*, was taken on a specimen collected September 13, 1953.

Ticks (Acarina). *Ixodes marxi* Banks was the only species of tick recorded from red squirrels in the Ithaca area. Specimens were taken from 36 squirrels and one nest. Eighteen adult females were collected in March, May, June, July, August, and September. Nymphs, numbering 58, were obtained in February, March, April, June, July, August, September, October, and November. Sixty-seven larvae were secured in February, June, August, September, October, November, and December. A nest examined in September yielded 4 adult males and 2 nymphs.

The majority of the ticks were attached to the inside of the pinna. As many as 12 specimens were taken on a single ear. They also attached to the head between the eye and ear and between the ears, shoulders, and upper arms. Five engorged specimens remained on one squirrel for at least three days without changing their position.

Lice (Anoplura). *Neohaematopinus sciurinus* (Mjöberg) was the only species of sucking louse encountered. Adults, immatures, and eggs were collected from 14 squirrels. A squirrel collected July 17, 1952 had an inflamed, glabrous area just above the elbow. Attached to this spot were two ticks and at the periphery were many lice. Seventeen were counted at the edge of the bare area and numerous others were moving about in the hairs a few millimeters away. Some had their bodies in close juxtaposition and may have been copulating. Many eggs were attached to the hairs in the vicinity. No lice or eggs were observed on other parts of the body.

Fleas (Siphonaptera). A total of 764 fleas were collected and identified. Of these, 622 were from animals taken in the Ithaca region, 66 from specimens obtained in northern portions of the state, and 76 from nests. A special effort was made to collect every flea from each of 186 specimens killed throughout the year. Immediately upon collection the squirrel was placed in a waxed paper bag. Fleas were obtained in the laboratory by placing the carcass in a white enamel pan or on a white sheet of paper beneath a desk lamp. Fleas would soon begin to leave the animal and could be picked off with forceps dipped in alcohol. Carefully combing the fur with a tooth brush aided in securing those remaining on the animal. An average number of 4.5 fleas per individual was obtained from the 137 (73.6%) of the 186 specimens that were infested. There was no significant sexual differences nor seasonal trends in the incidence of infestation or average number of fleas per squirrel. The highest number of fleas taken on a single individual in the Ithaca area was 43 (all *Orchopeas howardii*).

Eleven species of fleas were recorded. The numbers following the months of collection denote the number of squirrels from which fleas were taken.

Epitedia wenmanni (Rothschild). 8 females collected in February (4), March (1), May (1), and December (2).

Epitedia faceta (Rothschild). 6 collected (3 males, 3 females) in February (5), and March (1).

Tamiasciurus grandis (Rothschild). 2 females collected in June and September.

Ctenophthalmus pseudagyrtus (Baker). 2 females collected in April and May.

Orchopeas caedens durus (Jordan). This species was not taken on squirrels in the Ithaca region. On July 16, 1953, 6 females were collected from two red squirrels on Mt. Whiteface in Essex County, at an altitude of 4400 ft.

Orchopeas leucopus (Baker). 4 collected (2 males, 2 females) in February, May, June, and July.

Orchopeas howardii (Baker). 563 specimens collected (219 males, 344 females) during all months of the year. This is the characteristic flea of red squirrels in central New

York, although slight evidence suggests that it may be replaced by *O. caedens* in the north-eastern portions of the state. Females equalled or exceeded the number of males collected on individual squirrels in 91 (74%) of 123 cases. A greater number of females was collected in every month of the year except March. The division of the sexes of 45 specimens collected from several nests was 22 males and 23 females, suggesting that the consistent predominance of females on the animals is a reflection of a difference in habits between the sexes. Females may require more blood meals, which are necessary for the development of the eggs (Holland 1949). A tendency toward a similarly unbalanced sex ratio was exhibited by other species of fleas collected.

An indication of the proportion of fleas on an individual to those in the nest was obtained when an adult male was killed immediately after it left the nest. Three *Orchopeas howardii* were obtained from its body. The number of the same species collected in the nest was 22 (8 males, 14 females) and a number probably escaped. Three copulating pairs were among those secured.

Over 50 fleas of this species were collected by William Werner from a single red squirrel killed on Harbor Island in the St. Lawrence River, Jefferson County.

Ceratophyllus gallinae (Sehrank). 3 collected (1 male, 2 females) in March (2) and April. These were probably acquired by the squirrels through the use of dens formerly utilized by hole nesting birds.

Megabothris acerbus (Jordan). 1 male collected in December.

Monopsyllus vison (Baker). Next to *O. howardii* this species occurred most commonly on red squirrels in the Ithaca region. Thirty-two specimens (19 males, 13 females) were taken on squirrels in February (2), March (6), April (3), June (1), July (2), August (1), October (1), and December (3). On July 14, 1953, 6 males and 3 females were collected from a road-killed squirrel at Woodgate, Oneida County. A single female was obtained from another squirrel killed at Lake Placid, Essex County on July 16, 1953. Two Ithaca and one Adirondack nests yielded 31 specimens (11 males, 20 females).

Nosopsyllus fasciatus (Bose d'Antic). A single male was taken on a squirrel killed in the vicinity of a group of old farm buildings. It is a common flea of the Norway rat (*Rattus norvegicus*) and its occurrence on the red squirrel can probably be considered accidental.

SUMMARY

The southern red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), was studied from October 1950

to July 1953 in central New York. Observations were made primarily in Tompkins County in the vicinity of Ithaca. The most intensive field work was conducted from September 1951 through September 1952. In addition to numerous hours of field observation, a total of 575 squirrels were killed or live trapped. Conventional weights and measurements and data pertaining to molt, ectoparasites, reproductive condition, and stomach contents were obtained from autopsy of 440 specimens killed by various methods. Fifty-seven of 116 animals live trapped, marked, and released during home range studies were retrapped 180 times. Several hundred sight observations were also made on marked individuals in the field.

Mean external measurements of adults were: total length 310.2 mm, tail length 124.3 mm, body length 185.0 mm, and hind foot 48.0 mm. Adult males averaged 193.70 gms in weight. The mean weight of mature females was 188.80 gms. No trenchant sexual differences were indicated in any measurement. The variability of females was somewhat greater in 11 of 15 measurements taken.

Individual variation in winter and summer pelages of adults is apparently unrelated to sex or age. The juvenile coat differs in texture and other particulars from the adult pelage. Aberrantly colored individuals are rare. Adults molt the body pelage twice a year and the tail only once. The period of the spring molt is from late March to early July. The change is from the head caudad. The fall molt is in progress from late August to early December. Its inception and progress is the reverse of the spring molt. Spring juveniles undergo a complete molt in mid-summer, at an age of 12 to 15 weeks. Its course is similar to that of the adult spring molt except that the tail hairs are also replaced.

The various habitats in which the squirrels were found in the Ithaca region may be more or less arbitrarily categorized as 1) beech, maple, hemlock forests, 2) mixed hardwoods and scattered conifers, 3) coniferous plantations, 4) old orchards, 5) hedgerows, 6) park-like areas, and 7) edificarian. The first two types seemed to support the most stable populations, although not necessarily the highest.

Populations of 1.85, .96, and .72 squirrels/acre were obtained in three woodlots of mixed hardwoods, hemlock, and white pine. Densities of .62 and .85 squirrels/acre were recorded on an open 47 acre section of the Cornell University campus in the early summer of 1952 and 1953. An average of 1.8 and 2.1 squirrels/100 yds. were killed in a total of 2500 yds. of hedgerows during the winter and early spring of 1951-52. The lowest population specifically studied was .28 squirrels/acre on a 10.5 acre woodlot of second growth beech-maple-hemlock. Concentrations of individuals occasionally occurred in restricted sites near dwellings.

The nature of the food exhibits seasonal trends, the actual food species depending on the habitat and availability. Mast was a staple year-round food but was most important in fall, winter, and early spring.

Green plant material was a major item in April and May, while fleshy fruits figured prominently in the diet during June and July. Conifer seeds and fungus were frequently eaten during the late summer and early fall. Animal food was not commonly consumed. A single instance of predation on young birds was recorded. Food storing activities were most intense during the fall. Moisture is obtained from open water, succulent foods, snow or ice, or sap oozing from wounds in trees.

Peak stomach weights occurred between 10 a.m. and noon and 5 and 7 p.m., indicating two daily feeding periods. Heaviest stomachs averaged 19 gms; therefore a rough estimate of the daily weight of food ingested is 40 gms. Captives consumed an average of 12.6 to 14.2 gms of dry corn per day.

Results of field collecting and specific census studies showed the occurrence of two daily activity peaks. The animals are most active within 2 hours after sunrise and before sunset. Increased alimental and social activity account for the observed peaks. Approximately equal numbers were collected during clear and overcast days. Moderate to strong winds seemed to diminish activity or restrict it to the ground or sheltered locations. Fewer squirrels were taken when temperatures were below freezing, but individuals were active on the coldest days. Animals were often active during or right after light rain or snow but were not in evidence during heavy precipitation. Very low temperatures, high winds, and heavy snow effected the greatest reduction in activity.

The sex ratio of 458 adult and subadults collected by all methods was 102 males to 100 females. The balance of the sexes of live trapped animals was not significantly different. The sex ratio of 92 juveniles was 188 males to 100 females. Forty-two nest young were composed of 23 males and 19 females. Of 13 fetuses in which the sex could be determined, 6 were males and 7 females.

The season of reproduction can be considered to extend from January to October and to include two distinct breeding seasons, in late winter and mid-summer. Breeding at other times during the warmer months is apparently not common. The testes, prostate, and seminal vesicles were regressed from September to November. Enlargement of the testes was noted in late November and December. The prostate and seminal vesicles did not begin to develop until about a month later. The gonads of most males were fully developed from February to August. In 116 specimens, with only four exceptions, sperm were contained in the cauda epididymis of only those testes at least 15 mm long and 1000 mgs. A partial regression of the prostate and vesicles occurred in April and May, coincident with a sexually inactive period of the females.

The percentage of females in estrus was highest in February and March and June and July. Peaks of pregnancy occurred in March and April and July and August. The highest number of lactating individuals were encountered in April and May and August and September. It was possible to deter-

mine the approximate stage of the reproductive cycle from the gross appearance of the genital tract, external genitalia, and teats.

The relationship between the sexes is apparently promiscuous. Mating chases observed were composed of from two to seven squirrels. These occurred in the early morning and late afternoon and took place both on the ground and in the trees. A peculiar soft grunting note is characteristic of rutting activity. Copulation takes place on the ground or in the trees, the male often being towed about by the female.

Counts of placental scars, embryos, and nest young indicate a mean litter size of 4.5 (1-8). The mean number of young for 43 spring litters was 4.0, for 15 summer litters 5.3. Loss of ova and incidence of resorption were low. A number of adult females apparently produce two litters in a season; others may not breed until summer. Spring juveniles of the previous year apparently breed in late winter or early spring. A few summer juveniles may mate at this time, but most probably do not mature until summer. Males apparently mature earlier than females. By March, 91.3% of those collected were sexually active. No immature specimens were taken after April 7.

The gestation period is not definitely known but is estimated to be approximately 40 days. The young at birth is hairless except for the vibrissae and fine hairs on the chin and lips. The external auditory meatus becomes patent at about 18 days. The eyes open between 26 and 35 days. The pelage is almost completely developed at 40 days. Lower incisors appear above the gums at approximately 21 days, and the full permanent dentition is attained by 18 or 19 weeks. At the latter age, external and skeletal measurements fall within the range of the adult structures. Average adult weight is generally not reached until sometime later.

The young probably explore the nesting cavity as soon as the eyes are open and begin to make limited excursions from the nest when about six to seven weeks old. They are apparently weaned at seven to eight weeks but do not forage any distance from the home site until about 10 weeks. A somewhat loose association may obtain between the adult female and her offspring for a few weeks following weaning.

Leaf nests, tree cavities, fallen trees, rock piles, underground burrows, and man-made structures provided nesting facilities. Holes in trees were more heavily utilized than were outside nests. Underground burrows were noted in all habitats but were most commonly encountered in hedgerows. Non-parasitic arthropods collected from five leaf nests included centipedes, pseudoscorpions, spiders, beetles, chalcid wasps, Lepidoptera larvae, and Collembola.

The average size of 37 home ranges of adults and juveniles of both sexes on a 47 acre portion of the Cornell University campus varied from 2.73 to 6.03 acres. These studies were made in the early summer of 1952 and 1953 by a method involving observation of marked individuals with a minimum of live trapping. Home ranges of six adults inhabiting a heavily

wooded 10.3 acre plot were determined from trapping records over a 20 months period. Four males averaged .32 acres, and two females .44 acres. The marked differences in home range size between the two areas are probably due to the greater density of cover and food sources on the latter. Two specific cases of shifting of home range were noted, and evidence was obtained as to the effect of a particular food source on the shape of the home ranges of seven individuals. Ten of 100 squirrels marked on two study areas apparently occupied the same home area for periods ranging from 12 to 27 months.

Evidence of homing ability was obtained incidental to other studies. Three adults returned to their home areas from distances of 1600 to 2300 ft. Two juveniles returned from 1400 to 1800 ft.

Observations on territoriality suggest that red squirrels do not normally establish exclusive property rights over specific areas within the home range, and that territorial behavior is usually restricted to a small area encompassing a feeding station or particular den site over which an individual holds priority by reason of initial occupancy.

Loss of a portion of the tail was the commonest deformity noted. Of 247 adults examined for this condition, 20.2% had sustained some injury to the tail. Two cases of malocclusion and several minor skeletal defects were observed.

Thirteen squirrels were known to have lived a minimum of 16 months. Five were between 18 and 22 months of age, and three were at least two years old when last handled. Three others were from 27 to 31 months when last trapped, and one adult female was estimated to be 33 months when killed. Predation does not seem to be an important factor in mortality. Only one predator kill was found. Road kills account for some mortality, particularly among the young within a month of two of leaving the nest.

Endoparasites found in the few animals examined for them consisted of intestinal protozoa and tapeworm cysticerci. Carcasses were carefully examined for ectoparasites. Six species of mites, a single species each of tick, louse, and chigger, and 11 species of fleas were collected and identified.

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THE BIVOUAC OR TEMPORARY NEST AS AN ADAPTIVE FACTOR IN CERTAIN TERRESTRIAL SPECIES OF ARMY ANTS

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The American Museum of Natural History

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INTRODUCTION

The driver ants of the Old World and the army or legionary ants of the New World tropics form the distinctive subfamily Dorylinae in which all species are characterized by a carnivorous diet and a nomadic way of life. Another of their typical and prominent features is the large size of individual colonies, which seem to range from a minimum not far below 100,000 individuals in some species to hundreds of thousands or even millions in other species. These characteristics must have been closely interrelated in evolution, for as Wheeler (1928) has pointed out no ants or other social insects have managed to retain a nearly exclusively carnivorous diet and at the same time to support very large colonies with fixed nests. In the army ants, a diet consisting almost altogether if not entirely of the flesh of other animals has persisted during the evolution of a complex pattern of life in which the capacity for establishing permanent nests has been lost or very extensively modified.

Many references to doryline nests will be found in the literature, for Old World species by Savage (1847), Brauns (1901, 1903), Vosseler (1905) and Cohic (1947), for New World species by Belt (1874), Müller (1886), Wheeler (1900, 1913, 1921 and 1925), v. Ihering (1912), Gallardo (1915, 1920), Bruch (1916, 1923), Beebe (1919), Reichensperger (1930)

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and Schneirla (1933, 1938). Despite the potential significance of the problem from an ecological and behavioral standpoint, the references have been largely descriptive and introductory.

We propose to study the Eciton nest analytically with particular reference to its adaptive significance for the behavior pattern of the species.

An insect nest is definable as a situation within which the colony is sheltered and the brood is raised. Eciton nests or "bivouacs," although changeable in location and makeup, conform essentially to this definition. In the two species of the subgenus *Eciton* which form the basis for the present article, these shelters are formed of the ants' own bodies, without the manipulation of foreign materials (Fig. 2). These species and their close relatives are exceptional among the dorylines in that they establish their nests and carry out their daily raids almost entirely above the surface of the ground. Hence they may be termed "terrestrial." Other species in the American genus *Eciton*, as well as in the dorylines generally, are more or less strongly subterranean both in raiding and nesting.

In the terrestrial Eciton species *E. hamatum* and *E. burchelli*, to be discussed in this paper, two principal modes of life have been identified, according to distinctive differences in the functional and biological conditions of the colony (Schneirla 1933, 1938, 1949b). (This pattern in its important aspects is

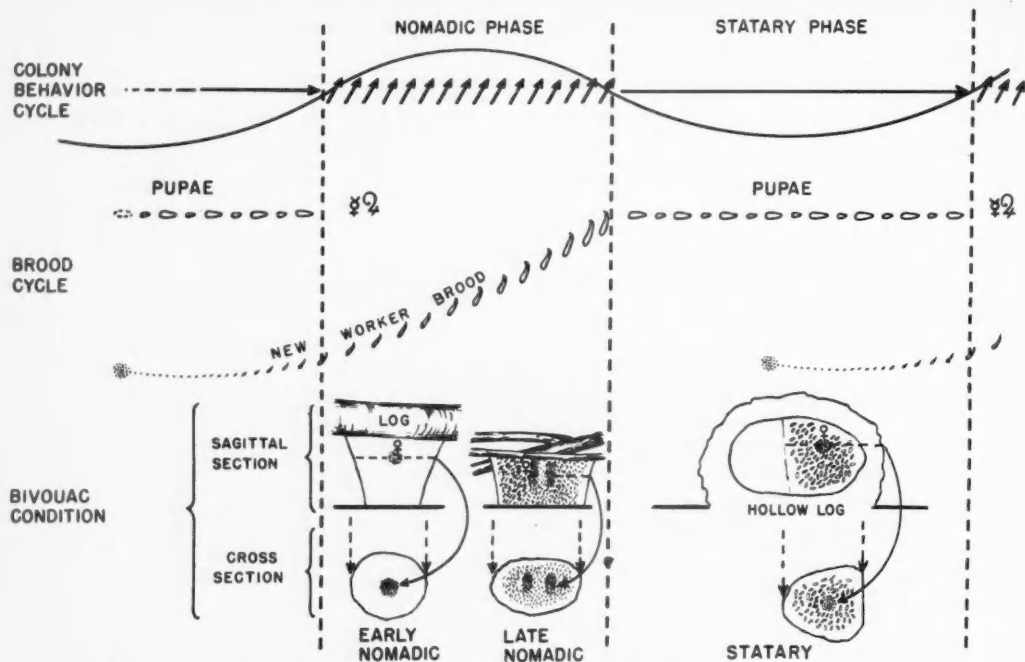


FIG. 1. Schema of principal variations in the bivouacs of terrestrial *Eciton* species in their concurrent relations to brood condition and colony behavior through the functional cycle.

Colony behavior: from the left—termination of a statary phase, then a complete nomadic-statary cycle followed by the beginning of a new cycle. Arrows represent successive changes of bivouac site with the emigrations of the nomadic phase.

Brood cycle: from the left—a full developmental period is represented, from delivery of eggs midway in a statary phase, through completion of larval development in the following nomadic phase, prepupal and pupal development in the following statary phase, to the appearance of a new brood population of callow workers ($\varphi\varphi$). The egg-laying and early larval development of a further brood coincides with the terminal developmental stages of the preceding brood.

Bivouac condition: left—placement of the larval brood in its early and late stages in the open bivouacs of the nomadic phase ($\varphi\varphi$, typical position of the queen); right—central placement of the new egg-larval brood in relation to the queen and the widely distributed pupal brood in the enclosed bivouac of the statary phase.

illustrated in Figure 1.) The first is the nomadic, marked by large daily raids of distinctive pattern, each ending after dusk in an emigration of the entire colony to a new site occupied during the next day. The nomadic condition, recurring regularly in distinct phases, typically lasts 16 or 17 days in *E. hamatum* before a change occurs, and from 12 to 15 days in *E. burchelli*. In colonies of these species each nomadic phase is followed by a statary phase, a more or less sedentary time in which daily raids are small or at times absent, and a single nesting site is held without emigrations. In *E. hamatum* a statary phase typically lasts 20 days, in *burchelli*, 21 days (Schneirla 1949; Schneirla & Brown 1950).

Investigations by the senior author (1933, 1938, 1944a, 1949a) have shown that in these two *Eciton* species the maintenance of each of these alternating phases, as well as the change from phase to phase, depends upon the developmental condition of the brood or broods present in the colony (Fig. 1). Thus a colony remains nomadic while a large brood in the

larval condition is present, but becomes statary precisely when this brood reaches larval maturity and becomes enclosed within cocoons; a further nomadic phase is started when this brood emerges as callow adults, continues while a new brood is passing through the larval stage, and so on. It is concluded that, consistent with an extension of the trophallaxis concept of Wheeler (1928), the entire basis of this cyclic phenomenon in the *Ecitons* rests upon the cumulative excitatory effect (chemical and tactual) of the current brood or broods upon the adult colony population (Schneirla 1938).

The ecological adjustments involved in the establishment and maintenance of fixed nests by the colonies of most species of ants (Wellenstein 1928; Gösswald 1938, 1941, 1951; Eidmann 1936; Westhoff & Westhoff 1942) cannot be closely paralleled by those prevailing in the *Ecitons*, with their nomadic way of life. The unique cyclic phenomena described above are found prerequisite to an understanding of *Eciton* nesting functions and their variations in

time. These matters are the subject of the present paper.

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The drawing for Fig. 1 was made by Mr. Walter Holmquist of the Illustrators Corps, American Museum of Natural History; drawings for Figures 4, 5, and 6 were made by Dr. Robert Brown; photographs for Figures 2 and 3-A were taken by the senior author; that for Figure 3-B by Mr. R. E. Logan of the Museum's Photographic Division.

METHODS

The findings reported here are based upon several periods of investigation on Barro Colorado Island, C. Z. Introductory studies of the bivouacs of *E. hamatum* and *burchelli* were conducted by the senior author in the rainy seasons of 1932, 1933, 1936, and 1938 (Schneirla 1933, 1938, 1944a). These studies were resumed in the dry season of 1946 (Schneirla 1949a) and in the dry season of 1948 further studies involving preliminary microclimatic measurement were carried out (Schneirla & Brown 1950) which were continued by the junior authors in the rainy season of 1949.¹

General methods developed for studying army-ant colonies have been reported in previous papers (Schneirla 1933, 1938, 1949b). The adaptation of these methods to the investigation of 1948 has been described by Schneirla & Brown (1950). To a considerable extent the latter investigation was planned to accommodate ecological and microclimatic studies concerning the Ecitons.

Continuous recordings of temperature and humidity conditions were made at representative locations in the forest, as well as at the laboratory clearing. For this purpose, two Bristol drum-type 7-day continuous recording hygrothermographs were used. For each test, these were prematched under identical atmospheric conditions. To gain some idea of variations in the general environment, both instruments were placed on the ground in places differing in some important respect (e.g., north vs. south hillside ex-

posure under similar cover and on the same contour). These instruments were also used to obtain records from specific situations which had been occupied by army-ant colonies. In this case, one instrument was inserted into the actual space previously occupied by a colony, when this could be done without any appreciable alteration of the situation (e.g., without cutting vines or removing brush). The second instrument, used as control, was placed nearby on the open forest floor as close as possible to the same contour.

Notes were kept in detail on the ecological and behavioral properties of colonies under study, and on the bivouacs themselves. These notes covered points ranging from nature of forest cover and of lower vegetation in the bivouac area to the specific location and properties of the bivouac itself. The more specific items would include nature of support and bivouac cover, degree of exposure, and pattern of the bivouac including the condition of its wall and interior at different times of day. In addition, the record always included items on colony behavior and condition of the brood.

With a modified cog psychrometer (Gray 1929), records were taken to sample relative humidity in the atmosphere surrounding each bivouac. These included records taken at distances of 1 m and 3 m from the bivouac, at a height of 1 m from the ground. Temperature was recorded at various spots outside and within the bivouac, with immersion-type mercury-in-glass thermometers (0-50°C, accurate to within at least 0.5°C). With these, atmospheric temperature was measured just above ground level, at bivouac-top level and at 1 m from the ground at points within 5 cm of the bivouac wall and at 1 m and 3 m from the bivouac. Temperature records were taken from points at bottom, middle, and top of the bivouac interior, both in the center and at various spots from just inside the wall to the center. The brood was localized as far as possible so that temperature readings from its central and marginal areas could be recorded as such. Ground temperature was taken at the bivouac base and at distances of 1 and 3 m with Weston dial-type thermometers.

Full-view and sectional sketches were made to scale of each bivouac investigated, so that the spot reached in each temperature reading could be recorded as accurately as possible.

An effort was made to obtain records from the same colony for different times of day as well as records for the same time on successive days. When records were taken through a period of numerous days, the general work schedule did not always permit visiting the colony at the same time of day. This matter proved to be a considerable handicap in the investigation of 1948. Therefore a principal aim of the 1949 investigation was to obtain records from particular colonies over periods of time, always at the same times of day.

AREA OF INVESTIGATION

General ecology. Barro Colorado is the largest of the islands in Gatun Lake, created in mid-Panama

¹ Further studies in this investigation were carried out by Dr. William B. Jackson (Jackson 1952) at Barro Colorado Island in the dry season of 1952 with the arrangement of the senior author.

through the damming of the Chagres River in 1914. It is roughly 2.5 mi. wide by 3 mi. long, and has a map area of nearly 7 sq. mi. bordered by a highly irregular shoreline with deep coves. Its highest point is 452 ft. above the level of Gatun Lake and 525 ft. above sea level. The island surface is very irregular, except for the central plateau, and is marked by many deep ravines radiating from the central area.

Ecological discussions of the Barro Colorado area have been offered by Allee (1926 a, b), Kenoyer (1929), Williams (1941) and others. With the rest of the Caribbean drainage of Panama, this area is located in the humid portion of the Lower Tropical Zone (Goldman 1921).

Except for a few small marginal clearings, the island is completely covered with a seasonal evergreen forest (Beard 1946; Richards 1952), both in its generally more rugged peripheral areas and its broad central plateau. The eastern part in general, as well as some scattered patches elsewhere, have a relatively young forest affording a lighter cover; elsewhere an older forest of heavier cover largely prevails. The relatively precipitous northern side of the island is reached directly by prevailing northerly winds which sweep across Gatun Lake; the gradual slope of the southern side is more wind-protected. Therefore the island may be characterized as an area of heterogeneous terrain which presents a considerable variety in microclimatic conditions relevant to the army ants.

Climatics: According to Chapel (1928), Panama and the Canal Zone occupy a position near the boundary of the Northeast Trade winds and the Equatorial Calms or Doldrums, and are "subject alternately during a portion of each year to weather characteristic to each of these wind belts, (providing) a seasonal change and dividing the year into the 'dry' and 'rainy' seasons. The distinguishing characteristics of these two seasons concern wind, humidity, clouds and rainfall but the temperature is much the same. In an average year an eight month period, May to December inclusive, has weather characteristic of the Doldrums. This is the 'Rainy' season, with light variable winds, high humidity, considerable cloudiness, and frequent heavy local rains, reinforced by occasional general rains. During four months of the year, January to April inclusive, the Northeast Trade winds increase in force and extent Southward over the Isthmus of Panama and usually a short distance beyond. This is the 'Dry' season, with fresh North and Northeast winds, drier air, less cloudiness, and with the rainfall largely confined to light showers carried inland from the sea."

Over a 15 year period from 1925 to 1939, the average monthly rainfall of Barro Colorado Island remained below a monthly total of 2 in. from January to March inclusive and 3 in. for April, but rose to levels approximating 13 in. for all other months except November, which averaged about 22 in. for the period (Schneirla 1949b). In 1948 and 1949,

when our studies were carried out, the distribution of rainfall through the year did not depart from the typical pattern in any important respect.

In general the rains of the wet season are more lasting and higher in intensity, those of the dry season lighter and more sporadic (Breder 1946; Clayton & Clayton 1947). In the dry season, a few heavier rains may account for the greatest part of a monthly total. In both seasons the heavier part of the daily total of rain falls during the daytime hours, most of this between noon and dusk. Mornings tend to be relatively clear. In this connection it is significant that the activities of colonies of the terrestrial army-ant species have a distinct diurnal routine, as described below.

With the facts concerning rainfall, the characteristic daily march of events in humidity and temperature on Barro Colorado should be outlined (see Results: Section 6). In the forest, during daytime hours from 10:00 A.M. to 4:00 P.M., higher atmospheric temperatures varying around 27°C generally prevail at the forest-floor level. Lower temperatures prevail at other times of day and always at night. Relative humidity generally remains high during the night and maintains its lowest level during morning hours; temperature remains low during the night and maintains its highest level (sometimes near 30°C) during the midday period. During February, in the dry season, near the forest floor relative humidities below 75% are characteristic in the afternoon, in contrast to readings above 80% at night; temperatures above 29°C are characteristic in the afternoon, in contrast to readings below 25°C from midnight to 8:00 A.M. A corresponding difference prevails during rainy months.

Three contrasts in available microclimates, selected from our records of temperature and humidity conditions in a variety of situations, are represented in Table 6. Evidence bearing on atmospheric conditions through the forest seems highly pertinent for understanding the activities of colonies of terrestrial Eciton species, which exhibit a distinct daily routine (Schneirla 1938, 1944a). In all such colonies, the daily raid begins at dawn and builds up during the morning, then shades in the afternoon into a modified pattern leading into emigration and consolidation of a new temporary nest during the evening and night (Schneirla 1938, 1945). For an understanding of the Eciton adaptations both the seasonal characteristics and the daily march of events in the general environment must be taken into account.

It is probable that the army-ant population of Barro Colorado Island has been largely isolated from that of the mainland for the 40 years since the area was sequestered. The sole possibility of a connection, through wind-carried males, is probably not a usual event in the terrestrial species. Colonies of more than a dozen species are commonly found in all parts of the island. Ordinarily there may be close to 50 colonies of each of the two principal terrestrial

species studied in this investigation (Schneirla & Brown 1950).

RESULTS

TERRESTRIAL BIVOUACS AND THEIR VARIATIONS

Types of bivouac. The temporary nest of these two *Eciton* species typically hangs from some supporting structure to the ground. When the physical situation is relatively simple, as when the colony hangs from the broad smooth under surface of a raised log through a clear space to level ground, the bivouac cluster tends to be a symmetrical modified cylinder with vertical central axis and with its diameter decreasing linearly from top to bottom. This pattern is subject to considerable variation, particularly in relation to environmental heterogeneity.

The cylindrical bivouac pattern (Figs. 2, 3) is the standard type for both *E. hamatum* and *burchelli* (Table 1.) Deviations from this pattern (Fig. 4) occur primarily in relation to the physical aspects of the situation, and secondarily in relation to the size and condition of the colony. Thus a "curtain" or a "half-cylinder" is likely to form when the clustering space has a partial wall, as under the side of a log which rests flat on the ground or in the inter-buttress space of a tree; a "compound" form results when the situation is broken and varied, as among low plants or brush; a "platter" type is formed when no ceiling is available save a low-lying support such as ground vines; a "plug" type when the cluster closes a cavity such as a mammal burrow or log interior; a "pouch" type when the ceiling is un-

usually far from the ground or other surface below and the base of the cluster hangs in midair.

In Table 1 we have classified into these convenient types a total of 238 bivouacs of *E. burchelli* and 397 of *E. hamatum* studied on Barro Colorado Island in four different rainy seasons and two dry seasons. These results are of interest not only from the standpoint of trends in bivouac pattern, but also for the question of variations in bivouacs according to season, colony condition, and species.

From the prevalence of cylindrical and compound type bivouacs in the nomadic phase, it is apparent that colonies of these species are most likely to hang to the ground from some form of ceiling, when the environment furnishes situations of this kind. It will be noticed that more plug bivouacs are formed by colonies of both species in the statary phase than when nomadic, because their clusters then tend to form within cavities such as hollow logs, in which



FIG. 2A. Time exposure of a cylindrical bivouac formed by a colony of *E. hamatum* in the mid-nomadic phase. The bivouac, approximately 37 cm. in diameter near the top, is represented as found expect for the removal of rubble and vines roundabout.



FIG. 2B. Terminal part of an elongated open nomadic bivouac formed by a colony of *E. hamatum* in the late part of a nomadic phase. A nearly mature larval brood was distributed throughout the bivouac (cf Figure 1), and is seen partially exposed where the wall has been breached with tweezers.

a cylinder becomes a "stopper" unless the inner diameter is large. Similarly, more pouch bivouacs are formed when colonies are statary, because the colonies then are prone to establish their nests in hollow trees. Of similar interest is the greater frequency of pouch bivouacs in *Eciton burchelli*, a species which bivouacs in elevated places much more frequently than does *E. hamatum*.

Bivouac situations. The results summarized in Table 2 indicate the variety of sites in which *Eciton* bivouacs are formed. The distinction of "exposed" and "sheltered" sites will be discussed later, as will variations dependent upon season and activity phase. The fact that exposed clusters form most frequently under logs, beneath vines or brush, or against tree buttresses, in that order, may partially express the relative frequency of these sites as against others in the environment. Collection of data for a com-

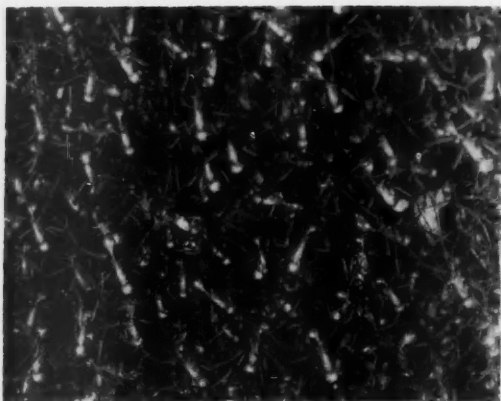


FIG. 3A. Close-up of a section of outer wall in a nomadic bivouac of *E. hamatum* (1.5 x).

parison on this basis was not feasible. Notwithstanding the great number of tree-base sites available in this environment, such places are utilized very infrequently in comparison with raised logs or vines. Physical characteristics affecting the ease or difficulty of forming clusters at different types of site may prove to be most important (Section 2).

THE PROCESS OF BIVOUAC ESTABLISHMENT

In the course of these investigations, the formation of more than 200 Eciton bivouacs has been studied. Based on an analysis of observational and test records, an account of the typical processes of bivouac-formation and their principal variations is presented in this section and the following two sections.

Behavioral prerequisites. When colonies of terrestrial Eciton species are installed in large wire nests in the laboratory, cylindrical clusters begin to form and are completed readily in dark and disturbance-free situations. These ants begin their hanging strands most readily under conditions of minimal extrinsic stimulation. Thus in the open they begin their new bivouacs most frequently after nightfall, when raiding has ceased and a monotonous movement of uniform columns prevails on the former raiding trails. There are still other preconditions.

Bivouacs seldom begin during hours of light; in fact, bivouac formation arises as a *sequel* to the daytime raid in these species. Actually, a maximal raid such as develops in the nomadic phase is essential as a basis (Schneirla 1933, 1938). The necessary events arise not simply through the presence of separate systems of trails formed during the day, but more specifically through the numerous main-trail junctions as centers of behavioral interaction. In the afternoon, as traffic conditions become increasingly complex on the trails, workers congregate and caches of booty are formed at the junctions. Travelers subject to persistent traffic interference gather at the main centers of impedance, where laden workers drop their booty loads if buffeted repeatedly in



FIG. 3B. Hanging strands typical of early stages of bivouac formation, with workers joined together by tarsal leg hooks, formed by *E. hamatum* introduced to a laboratory nest.

the approach. Ants surging out from the bivouac, reexcited after the midday siesta or depression interval (Schneirla 1938, 1949b), offer great opposition to return traffic. In the raiding system of *E. hamatum*, in the course of time one of the three principal trails is typically dominated by this exodus. As this process occurs, the trail junctions are certain to become areas of traffic friction and confusion. The aggregations of workers and heaps of booty which form at such "confusion centers" play an important part in the eventual production of a biv-

TABLE 1. Types of bivouac in relation to colony condition and season.

Bivouac type	<i>Eciton burchelli</i>							
	DRY SEASON				RAINY SEASON			
	Nomadic		Statory		Nomadic		Statory	
	No.	%	No.	%	No.	%	No.	%
Cylinder.....	73	46	1	4	24	50	2	12
Compound.....	18	12	0	0	3	6	3	19
Pouch.....	15	10	10	43	9	19	8	50
Curtain.....	12	8	1	4	4	8	0	0
Plug.....	17	11	10	43	4	8	3	19
Others.....	16	9	1	4	4	8	0	0
Total.....	151	..	23	..	48	..	16	..

Bivouac type	<i>Eciton hamatum</i>							
	DRY SEASON				RAINY SEASON			
	Nomadic		Statory		Nomadic		Statory	
	No.	%	No.	%	No.	%	No.	%
Cylinder.....	120	59	14	36	89	69	11	42
Compound.....	13	6	1	3	16	13	0	0
Pouch.....	1	1	1	3	0	0	4	16
Curtain.....	15	7	0	0	10	8	2	8
Plug.....	21	10	13	33	3	2	8	30
Others.....	34	17	10	25	10	8	1	4
Total.....	204	..	39	..	128	..	26	..

TABLE 2. Types of bivouac situations utilized by Eciton colonies on Barro Colorado Island.

Type of Site	<i>Eciton burchelli</i>				<i>Eciton hamatum</i>			
	DRY SEASON		RAINY SEASON		DRY SEASON		RAINY SEASON	
	No-madic	Statory	No-madic	Statory	No-madic	Statory	No-madic	Statory
"Exposed"								
1. Beneath log.....	53	1	16	0	102	8	54	9
2. Under vines or brush.....	27	1	10	2	42	1	45	1
3. Miscellaneous... (e.g., under rock edges, overhanging banks, tree buttresses)	26	2	15	1	32	4	26	1
Total "exposed".....	106	4	41	3	176	13	125	11
"Sheltered"								
4. In tree hollow.....	15	14	6	13	0	1	0	5
5. In hollow log.....	12	8	3	5	13	13	3	10
6. Subterranean.....	13	27	0	0	13	8	0	1
7. Base of hollow tree.....	6	3	0	0	2	3	1	0
Total "sheltered".....	46	52	9	18	28	25	4	16
Total ("exposed" and "sheltered").....	152	56	50	21	204	38	129	27
% "exposed".....	69.7	7.1	82.0	14.3	86.3	34.2	96.9	40.7

ouac, chiefly because they represent points of potential large-scale stoppage.

The bivouac as sequel to a maximal raid. As noted, Eciton workers cluster when extrinsic stimulation is low and when movement is repeatedly impeded. These conditions arise on the principal route of exodus as dusk approaches. Then raiding stops and former raiders throng the trails. The resulting convergent drift of traffic toward the base trail of the raiding system creates major collision points at trail junctions where the centripetal drift meets the persistent exodus from the bivouac. Disoriented travelers accumulate in rapidly increasing numbers at these centers, and cache heaps of booty may grow considerably.

A new stage arises in the process when brood transport from the bivouac begins later in the exodus. Larva carriers, when their progress is impeded at collision points, tend to drop their burdens, generally upon the accumulated booty. Large scale feeding then typically arises in colonies with fairly mature larval broods, a condition which tends to increase and prolong the local congestions. Numerous congestion-point gatherings of this type form and disappear successively in the aftermath of a nomadic-phase raid.

Although the continuing exodus from the bivouac is a primary factor in the formation of such gatherings, it is also the cause of their eventual breakdown. This process typically begins at points nearer the bivouac and advances progressively toward peripheral

junction points. Although varied in its form, the change is inevitably introduced through a persistent outward pressure exerted by the exodus. Working against a typically variable pressure of centripetal columns entering the junction zones from the peripheral side, the steady pressure of the exodus finally breaks a way through the mass. When it dominates the main trail with a stream of traffic at the outer side of the junction gathering, the exodus usually requires little time to overcome opposition. Consequently, as a rule the direction of traffic is then soon reversed all of the way to the next congestion center on the route.

This process of successive penetrations and traffic reversals is subject to variation in time and pattern, particularly in dependence upon the tempo and force of resistance which centripetal traffic presents to the exodus. With a strong and protracted centripetal opposition, the exodus may be reversed temporarily or may be permanently reversed and forced into another trail system. When both the exodus and opposing forces exert a continuous strong pressure upon a congestion point, a further development may arise. One of the blocked columns, diverted at some point in the congestion center by opposing traffic, breaks out laterally. Into this lateral eruption the other traffic stream, the previous blocking agent, may be drawn in some manner. In the darkness, the columns crowd out in a broad-headed or branching pseudopod advance, in which the vanguard moves variably and hesitantly while pressed on from the rear. The ground is unlikely to be well saturated

with Eciton chemical, for the eruption may occur on a minor branch line of the daytime raiding. The rush usually is rather sudden however, and in considerable numbers, so that it soon becomes congested where some of its pseudopodic branches reach and mount nearby obstacles such as logs or brush. These occurrences open the way for a new stage, to be described presently.

In a nomadic movement it is not unusual to observe numerous developments of this kind, arising at successive trail junctions as the exodus sweeps toward the periphery of the former raiding system. Often two or more exist simultaneously. Numerous lateral eruptions occur in succession, but dissipate readily when basal traffic changes drain ants away at the source. Traffic changes, whereby the exodus comes to dominate the route beyond a congested point, often lead to the breakdown of local developments which have attained the status of young bivouacs.

Although at times the potential bivouac cluster begins relatively early and may be continued without much interruption to completion, as a rule the process is variable and difficult to predict. Its progress frequently depends upon traffic conditions, as discussed in part above, and upon the topography of trail-junction localities. As an illustration of the second point, unless a pseudopodic eruption soon hits upon a place at which clusters can form rapidly, traffic first becomes congested and disorganized, then reverses. A growing cluster can absorb great numbers and thereby maintain the forward movement by draining it away, but an eruption unabsorbed by clustering usually does not continue long.

At times, all of the clusters which may begin at separate congestion points are dissipated in these ways, and the exodus by degrees sweeps onward to reach and even to pass beyond the forefront of the day's raiding zone. In that case, the eventual bivouac is established in a manner resembling that arising through a pseudopodic-eruption column.

Building the bivouac cluster. Bivouac formation as a specific process begins with the formation of hanging clusters at concentration points after dusk. These clusters typically begin in the following manner. As workers in a pseudopodic advance run circuitously over a log or some other surface which they have mounted, some of them pass over the edge to an undercut surface. Under these conditions, Eciton workers are likely to stop when headed downward, with the front pairs of legs free, so the the body actually hangs for a moment at least. From this hanging position, anchored by the tarsal hooks of the rear legs, the worker may return promptly to the running posture. However, if in the meantime a newcomer has run down along the extended body and has stretched out in her turn, hooked from the ant above, the latter remains extended. If further ants then can run down and become hooked in turn, extending the chain, the anchor members become quiescent and hang in place (Figure 3-B). If re-

cruits arrive rapidly in sufficient numbers, the thread-like chain soon widens from its base into a rope, and new chains are started nearby.

Since the cluster thus builds downward from an elevated surface, the anchor members hang head downward from the natural ceiling, and further members are most likely to hang by the large rear leg hooks in a similar posture, since they in turn join the cluster by running down it from above. These conditions, rather than a specific predisposition for "negative geotropism" as Wheeler (1900) supposed, seem to be responsible for the prevalent head downward position of workers forming the main structure of a bivouac wall (Fig. 3).

If the flow of traffic continues to the spot, other chains are started close by and quickly extended downward. As the weight of each chain grows, the sharp hooks of the basal members are fastened more firmly. Also, the pull of ant upon ant has the effect of stretching out the body between legs pulled out oppositely. The evident result is a specific reaction suggesting a reflex immobilization, whereby the fastened basal parts of the chain become quiescent except for antennal and other minor actions. We favor the interpretation suggested by Schips (1901), who compared the immobilization of ants in the hanging strands of *Dorylus nigricans* with the condition of "hypnotic stiffness" known in many other insects.

Clustering and the formation of festoons and fringes of ants usually begins at separate places in the same locality. However, the few adjacent ones that progress most rapidly may determine the pattern of general growth by draining in the largest number of ants at their bases and thus indirectly facilitating the breakdown of isolated strands slower in development. Strands close together have an advantage since they tend to grow together into a larger and stronger mass, whereas isolated threads and tendrils tend to break through their own weight or to be otherwise abandoned. When festoons are formed close together, they are soon joined as newcomers hook into the interspaces. When the distance from ceiling to ground is not too great, thin strands may reach the ground independently; over greater vertical distances, independently growing strands may break repeatedly before they are joined into a more substantial structure. It is the limited strength of the initial strands which evidently restricts the height of ceilings from which bivouac structures can be built to the ground. The maximum is not much more than 28 cm in *E. hamatum*, but somewhat more in *burchelli*, which can form stronger strands more rapidly than can *hamatum*. In elevated places, *burchelli* frequently makes bulbs or pouches, which are in essence cylindrical clusters finished off without support at the base; *hamatum* seldom does this (Table 1).

Bivouac cylinders develop most commonly by the addition of strands at the circumference of a loose central core of festoons. Outer strands as they

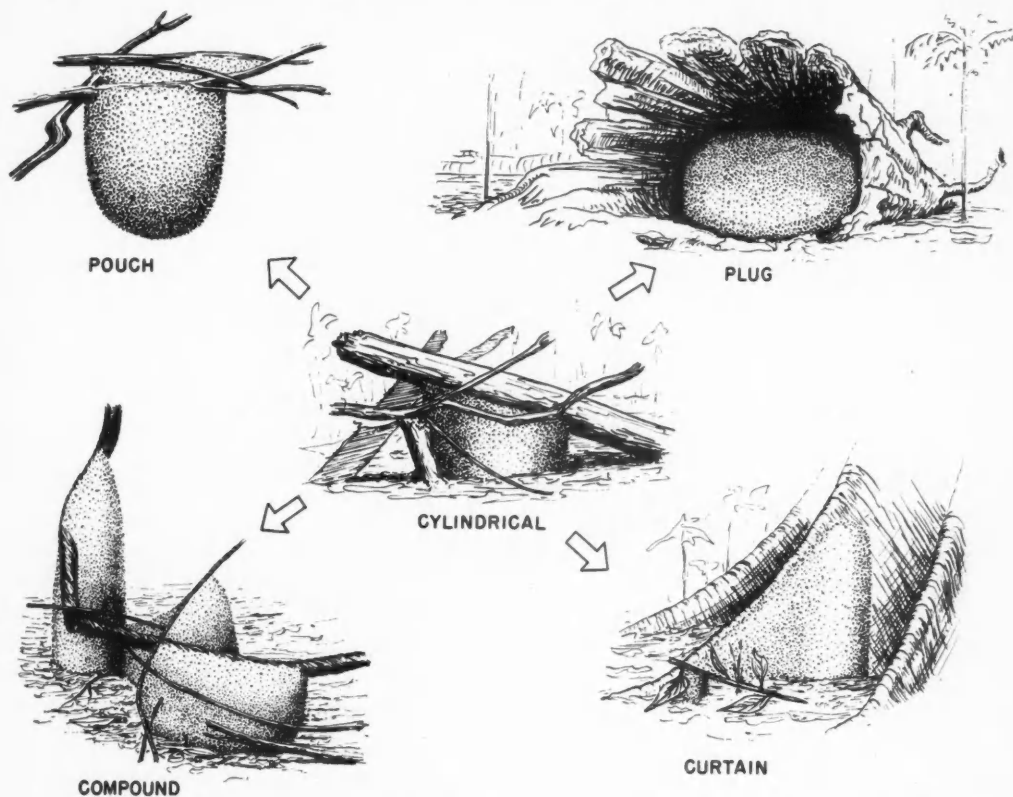


FIG. 4. The principal types of bivouac in the predominantly terrestrial species of *Eciton*. *Cylindrical*: the representative open formation of the nomadic phase; *curtain*: frequently formed against buttressed tree roots or from overhanging surfaces to the ground; *compound*: the complex type of the nomadic phase; *pouch*: formed more often by *E. burchelli* than by *hamatum*, usually in the statary phase, and not infrequently in open elevated positions; *plug*: characteristically formed by colonies of both species within hollow logs or in subterranean cavities in the statary phase. (See Tables 1 and 2).

lengthen are pulled inward toward the core by ants linking into the gap. This process, readily identified, would appear to account for the fact that the circular outer wall of a completed cylindrical bivouac in these species commonly tapers inward from top to bottom (Fig. 2). Bivouac in these species tend to be circular in cross-section and symmetrical with respect to the inward slope of their walls from top to bottom. This results from the fact that they commonly grow through the addition of strands symmetrically around the margin of a circular core. Since the influence of gravity tends to be equal at all points on the circumference during construction, the main axis always approximates a true vertical.

CHANGES IN THE STRUCTURE OF ESTABLISHED BIVOUACS

Secondary changes in form or position. In the forest, nomadic bivouac clusters established at the end of one day generally are held without major change through the following day. However, limited changes in form or even in position may occur, demonstrably under the effect of extrinsic conditions.

A disturbing effect such as very bright light on one side of a cylinder noticeably causes a general agitation of ants in the affected locality; individuals free themselves, move about circuitously, and soon have shifted away from the place. Thus, where the disturbance acts, part of the cluster literally melts away and the opposite side or another part soon bulges correspondingly as the displaced members settle there. In such ways, under natural conditions, bivouac clusters may change their shape or even their location if subjected to sufficient disturbance over a sufficient time. Typical causes of such changes are heat and bright light as from sun flecks, or the local action of rain. Frequently the shift can be stopped by appropriately shielding the bivouac from the disturbance. With colonies in the laboratory, housed in nests of mesh wire in which they form regular cylindrical bivouacs, reactions of this kind can be demonstrated readily through the controlled local action of bright light or excessive heat.

Similar reactions commonly account for minor changes in statary bivouacs. Although such bivouacs

almost always hold to the same locality (e.g., within the same hollow log), at times definite changes in form and even complete displacements in position may occur. Continuous observations indicate that such changes come about through a gradual evacuation of ants from the side of persistent unilateral disturbance, while it persists. At times a lasting general disturbance may set off a limited displacement of the entire cluster. For example, one colony of *E. hamatum* (Schneirla 1949b) which happened to settle (as statary) in a stump cavity opposite a statary colony of *E. praedator*, after three days moved about 6m into the hollow interior of an adjacent log. Clear signs of friction between the two neighboring colonies preceded the move.

Regular diurnal changes in bivouacs. Changes of a somewhat different nature normally occur in established bivouacs as a part of the daily routine. These are more pronounced in nomadic bivouacs than in statary, and may be described for the former type.

After the last ants have moved into a new nomadic bivouac in the evening or later in the night, the structure settles into a relatively quiescent condition in the course of time. The outer wall becomes rather close-meshed and uniform throughout its extent, without apertures, and usually there is a minimum of externally visible movement. Indications are that, within, feeding activities centering about the brood proceed during much of the night.

At dawn, ants on the surface are aroused by the first light (Schneirla 1940) and soon begin to stream out upon the ground in a rapidly growing foray. Typically the first ants to leave in large numbers take their exit from the bottom of the cluster. First the lower wall is thinned out as workers leave from the interstices, but, within an hour or two, units of the more basic wall structure near the bottom have unhooked themselves and left. As a result, the bottom of the bivouac presently becomes undercut, so that by mid-morning the bivouac often has become literally a pouch with ragged festoons hanging from it to the ground.

Typically the entire outer wall of the bivouac has thinned out after mid-morning, so that the basic meshwork of interlaced strands can be seen, with small gaps here and there. Through these holes, returning raiders carry their booty into the bivouac. Usually the upper half of the bivouac retains a closer fabric in its wall, by losing fewer ants to the raiding than does the lower part.

During midday hours, the upper part of the cluster acquires a somewhat closer fabric as ants rejoin the mass and remain in its wall during the hottest and brightest part of day. In the early afternoon, an extensive exodus begins as the midday period of siesta is replaced by a resurgence of activity. The cluster steadily loses ants to the continuing exodus, first from the lower wall and interior and then from upper parts. At length, usually after dusk, the process of drainage has reached the point of brood transport. When the larval brood is very young this point is

not reached until late in the movement, since the brood then is concentrated in the upper center of the mass (Fig. 1). This brood, transported in packets, consequently is moved as a rule only when the new bivouac is well advanced in construction. When the larval brood is older, and more widely distributed in the bivouac (Fig. 1), the carrying of brood begins relatively early in the emigration. These secondary differences in the daily routine all have their significance for the construction of the new bivouac.

BIVOUAC SITUATION AND ACTIVITY PHASE

Relative exposure of bivouacs. A hypothesis which we wish to examine concerns the relation of differences in the degree of exposure of bivouacs to differences in colony condition. A distinct impression is soon gained that in these terrestrial species, nests established in the nomadic phase are largely exposed to the general atmosphere and may be termed "open," whereas nests in the statary phase are typically established within a physical shell such as a tree or hollow log, and may be termed "sheltered" (Schneirla 1933). In the bivouacs of both phases, brood and queen are of course given a very appreciable protection by a mass of clustered ants enclosing them; the difference is that in the statary bivouac still further shelter, from a physical surrounding wall (or perhaps from its ecological equivalent), is available.

This hypothesis may be tested by an examination of situations in which clusters were formed in the two activity phases. In Table 3 we have classified 398 recorded bivouacs of *E. hamatum* and 276 of *E. burchelli* (the total studied in five rainy seasons and three dry seasons) according to whether the mass of ants was clearly exposed to the general atmosphere or was enclosed by a physical wall. A bivouac was classified as "sheltered" when it was mainly or entirely out of sight within a cavity such as the interior of a hollow tree or hollow log, as "exposed" when its outer wall was clearly in the open and readily seen for more than half of its circumference. Doubtful cases, excluded, were less than one per cent of the total.

Table 3 shows that for nomadic colonies of *E. hamatum*, 97% of the bivouacs in the rainy season and 86% in the dry season were classified as "ex-

TABLE 3. Frequency of exposed bivouacs in the two seasons.

Season	Species	Nomadic		Statory	
		Number of sites	% exposed	Number of sites	% exposed
Rainy	<i>E. hamatum</i>	129	97	27	41
	<i>E. burchelli</i>	50	82	21	14
Dry	<i>E. hamatum</i>	214	86	38	34
	<i>E. burchelli</i>	152	69	31	12

posed"; for nomadic colonies of *E. burchelli*, 82% of rainy season bivouacs and 69% of dry season bivouacs were "exposed." The corresponding values for statary colonies are very considerably smaller for both species in both seasons. For both species, in both seasons, it is clear that nomadic colonies tend to have exposed bivouacs, whereas statary colonies tend to have sheltered bivouacs. The difference is illustrated in Fig. 1.

The shift from open to enclosed sites typically is a striking one in both species, as is its reverse, when a change of activity phase occurs. A representative case is afforded by colony '46H-B, *E. hamatum*, under continuous study for 115 days (Schneirla 1949b). In its first observed nomadic phase of 16 days this colony with but one partial exception formed largely exposed bivouacs, then passed through a statary phase of 21 days completely enclosed within a hollow log, next passed through a further nomadic phase of 17 days with only one unexposed bivouac cluster, next a further statary phase of 20 days out of sight beneath a large buried tree root, and so on for a third cycle. In most cases brood samples were readily taken from nomadic bivouacs simply by puncturing the exposed bivouac wall, whereas in the absence of heavy engineering equipment this was impossible in the first two statary phases and also through most of the third.

In Table 3 it is seen that in the dry season exposed bivouacs are fewer in both phases than in the rainy season. *E. hamatum* had 11% fewer in the nomadic phase and 7% fewer in the statary, and *burchelli* 13% fewer in the nomadic but not a significantly smaller number in the statary phase during the dry season.

Subterranean bivouacs in terrestrial Eciton species. In other species of this subgenus, such as *E. rogeri* and *E. vagans*, none but subterranean or well secluded bivouacs have been found at any time on Barro Colorado Island although more exposed bivouacs of these species were observed under other conditions in Southern Mexico (Schneirla 1947). It will be interesting to examine our results for the two clearly terrestrial species under study, with respect to the use of underground bivouac sites such as mammal burrows.

The terrestrial species also utilize subterranean sites, as is shown by the results summarized in Table 4. This is only in a limited and secondary way, however. First of all, colonies of both species tend to go underground with appreciable frequency when statary, but not when nomadic. Thus for *E. hamatum*, there was a negligible frequency of subterranean bivouacs among the total of 342 recorded for the nomadic phase, whereas among 88 statary bivouacs on record, 13% were subterranean in the rainy season and 37% in the dry season. A less prominent difference appears in the case of *burchelli*.

A seasonal difference is outstanding in these results. Although in the rainy season no subterranean

TABLE 4. Subterranean bivouacs in *Eciton hamatum* and *E. burchelli*.

Season	Species	Nomadic		Statary	
		Number of sites	% underground	Number of sites	% underground
Rainy	<i>E. hamatum</i>	129	0	31	13
	<i>E. burchelli</i>	50	0	23	0
Dry	<i>E. hamatum</i>	213	3	57	37
	<i>E. burchelli</i>	162	6	45	15

sites were recorded for nomadic colonies in either species, in the dry season, in contrast to an occasional nomadic record, there was a very appreciable frequency in statary colonies. The seasonal difference is unmistakable in both species.

Table 4 also indicates a species difference in the frequency of subterranean bivouacs. Although no such bivouacs were recorded for *E. burchelli* in the rainy season, a considerable number was found in the case of *hamatum*. In the dry season they occurred in *burchelli* colonies, but only about half as frequently as in *hamatum*. These results may be contrasted with our findings for elevated bivouac sites.

Elevated bivouacs in terrestrial Eciton species. A most striking difference in the bivouac locations of doryline species is their position with respect to the ground level. For while we seldom find the bivouacs of *Eciton hamatum* and *burchelli* in subterranean places, those of *E. rogeri* and *vagans* (of *Eciton s. str.*) are seldom and those of *E. (Neiv.) pilosum* and *E. (Lab.) praedator* and *cocum* are almost never exposed above the surface of the ground. The results in Table 5 indicate on the other hand that the bivouacs of *E. hamatum* and *burchelli* not infrequently are established in elevated positions.

Although these two *Eciton* species are properly termed "terrestrial" because both carry out most of their activities on or above the surface of the ground, the results for subterranean nesting indicate that this characteristic is relative. Since both species conduct the greatest part of their raiding activities on the forest floor, but at the same time frequently extend their columns into the lower and even higher

TABLE 5. Species differences in number and frequency of elevated bivouacs.

Season	Phase	E. HAMATUM				E. BURCHELLI			
		On ground	Up to 1 meter	Above 1 meter	% elevated	On ground	Up to 1 meter	Above 1 meter	% elevated
Rainy	Nomadic	127	2	0	2	35	11	4	30
	Statary	21	6	3	32	0	5	18	100
Dry	Nomadic	205	9	0	4	129	21	12	20
	Statary	56	10	1	16	17	6	12	51
Total.....		409	31			181	89		

vegetation, it will be interesting to see how often their nests are formed above the specific zone of the forest floor.

From Table 5 we see that first of all both species tend to establish elevated bivouacs more frequently when statary than when nomadic. Although in our records for the rainy season, *E. hamatum* had elevated bivouacs in only 2% of the nomadic cases, 32% of statary bivouacs in this species were elevated. In *E. burchelli*, on the other hand, 30% of the nomadic bivouacs and 100% of statary bivouacs in the rainy season were elevated. Similar species differences, although less pronounced, are indicated for the dry season.

In both of these species, it will be noted in Table 5 that elevated bivouacs were on the whole much more frequent in the rainy season. A substantial increase is indicated for *E. burchelli* in both phases, for *E. hamatum* in the statary phase, as compared with the dry season. It will be seen, in comparison with Tables 3 and 4, that with the decreased frequency of elevated bivouacs in the dry season, there are also fewer exposed bivouacs and more subterranean bivouacs in that season. From the rainy to the dry season, both species therefore tend to establish their bivouacs at a lower level.

In Table 5 a clear difference is indicated between the two species in their tendency for elevated bivouacs. Elevated sites are occupied by *E. burchelli* more frequently in both activity phases and in both seasons than by *E. hamatum*. Altogether, *burchelli* had 89 elevated bivouacs or 33% in a total of 270, whereas *hamatum* had 31 elevated bivouacs or only 7% in a total of 440.

The greater proclivity of *burchelli* for elevated sites is emphasized when the relative height of bivouacs above the surface of the ground is taken into account. Although only 4 of 31 elevated bivouacs in *hamatum*, or 13%, were established more than 1m above the ground level, in a total of 89 elevated bivouacs established by *burchelli* colonies, 46 or 52% were at heights greater than 1m. Under all conditions, the highest bivouac locations were taken by *burchelli* colonies. Bivouacs at heights greater than 8m were recorded for this species on six occasions in the dry season, although only once (a statary nest) in the rainy season. One statary bivouac established by a *burchelli* colony in the rainy season (in a tall, lightning-split hollow tree) was nearly 20m from the ground. The tendency of *burchelli* colonies to go aloft in their bivouac-ing, and often for considerable distances, is unmatched among the dorylines.

RELATIONSHIP OF THE ECITON BROOD TO THE BIVOUAC

Energizing function of the Eciton brood. Every functional colony of these two Eciton species, at all times, has a large brood of developing individuals in its midst, and at distinct and regularly recurrent times two such broods are present. Since these broods are within the bivouac virtually all of the

time, the bivouac must of course be considered the principal environment governing their development.

For convenience in presenting some preliminary evidence on these relationships, the nature of the Eciton brood and its developmental stages may be reviewed briefly. The summary of the time relations of brood development and the colony activity cycle in Fig. 1 refers to the worker broods produced in regular succession throughout the year. In these species the worker brood is always a specific unitary population of great size (more than 30,000 individuals in *E. hamatum* and 50,000 in *burchelli*, at a conservative estimate) and at any one time all of its members are at essentially the same stage of development. There are always regular individual differences in size and polymorphic type. For example in colony '49 H-34 (*E. hamatum*), in a sample taken on the sixth nomadic day body length ranged from 1.55 to 7.28mm, and in a sample taken on the 14th nomadic day from 4.65 to 10.4 mm, the larger extreme potential major workers or soldiers, the smaller potential minor workers.

We have pointed out that the capacity of the brood to energize the colony is a very fundamental factor in the life of an Eciton colony (Schneirla 1938, 1949b). This role changes, as we have emphasized, according to the developmental condition of the brood. The critical function of the brood in the entire life of the colony is expressed by the changes that appear both in colony behavior and in the bivouac, according to the developmental condition of the brood.

Situation of the brood in the bivouac. The position of the worker brood in the bivouac is critical for this problem. With only secondary variations, the brood tends to be centered in the upper part of the bivouac cluster below the queen (Fig. 1). Changes in its position with developmental stage may be described in terms of conditions at four well-separated times: 1) within the period of a few days during and just after the laying of eggs, the brood usually is in a single large bolus supported among strands of workers in the upper center of the bivouac just below the position of the queen; 2) early in the nomadic phase, the brood is separated into a few central boluses (composed of the least advanced members, newly hatched eggs and youngest larvae) and a few strands located farther out from the center, the most advanced larvae in small packets; 3) in the latter part of the nomadic phase, the smallest (i.e., youngest) larvae in the brood hang in strands nearest the center, there are smaller strands or packets of older larvae farther out, and nearest the periphery the older larvae lie in small heaps in alveolar spaces or are held individually by workers. Thus during larval development the brood occupies an expanding area in the bivouac and is typically arranged concentrically in the upper center with the largest members marginally and the smallest centrally (Fig. 1). When the larval

brood reaches maturity, its largest and most advanced members are situated in the bivouac wall itself, held individually by workers. 4) In the statary phase, the bulky cocoons of the enclosed pupal brood are distributed throughout all but the lowest parts of the cluster, generally in heaps of variable size in spaces among the strands of hanging workers. After the eggs of the new brood have been laid midway in the statary phase, they are located in a large bolus in the upper center of the bivouac, as described under '1' above.

Thus from a restricted area in the upper center of the bivouac the Eciton brood as it grows to larval maturity comes to occupy an increasingly large part of the interior. In an established nomadic bivouac the brood is distributed roughly according to body size. At any one stage, whether early (when concentrated centrally) or later (when expanded through the bivouac) the brood exhibits a gradation in its arrangement, with the smallest individuals located near the center and largest individuals correspondingly farther toward the periphery in relation to size. This gradient however is not a simple one, since from the dense and central concentration of the smallest individuals the number per unit area decreases first sharply, then more gradually to the sparsest distributions of large individuals in the periphery. As a consequence, the problem of taking randomized samples from worker broods in the bivouac is a difficult one at all stages.

Adaptive results illustrating normal intra-bivouac conditions. For a better picture of conditions within a bivouac, some apparent adaptive outcomes related to the typical pattern of brood distribution may be cited. Generally speaking, at all stages of development the largest larvae seem more likely to receive the macerated remnants of the large food objects (e.g., in *E. hamatum*, the large pupae and larvae among the booty), the smallest larvae the more reduced sizes (e.g., in *hamatum*, the smaller captured pupae and larvae, and the eggs). In relation to this condition, there is less transport of the larger objects through the tangle of the bivouac interior. On the other hand, the smaller ants with their smaller burdens are able to slip rather easily to and within the bivouac center.

Even when the brood is very young and restricted to a single central bolus, a similar advantage prevails. The newly hatched eggs and embryos at the center of the mass are licked and handled by the minim workers, the largest individuals in the outer areas (i.e., larvae which have begun to feed) generally are attended by larger workers minor, which could not move readily through the central part of the bolus.

When the larval brood nears maturity, the largest individuals (i.e., potential workers major) are first to cease feeding and to begin their spinning. At this time they are generally carried from the bivouac to a place close by, where they are laid in wood dust or other detritus which soon covers them, and in

which they are able to spin. Smaller-sized individuals begin their spinning at correspondingly later times, and are treated similarly. Obviously, the typical brood arrangement means that the largest larvae have to be carried only a short distance through the bivouac, whereas the smallest ones, which can be carried most easily through the tangle of bodies, are the ones subjected to the longer hauls from near the center of the bivouac.

A comparable advantage is gained when the enclosed pupal brood is nearly mature and begins to emerge from cocoons. The largest cocoons, situated peripherally, contain workers major and larger intermediates, which reach full maturity soonest and are removed first. Then the bulky cases of these individuals need be carried only a relatively short distance to the bivouac edge, from which large numbers of the empty cases drop to the ground.

THE MICROCLIMATES ENCOUNTERED BY TERRESTRIAL ECITONS

Measurements were made of the relative humidity and temperature of the air layer approximately 15cm above the forest floor. This procedure was considered necessary to obtain a background for a study of bivouac thermodynamics. It also yielded a more quantitative description of atmospheric conditions encountered by the terrestrial Ecitons in the course of their daily activities.

The instruments used were two Bristol drum-type continuous recording hygrothermographs. Records were taken for five consecutive days in each location tested. During the records the instruments were not moved. Each instrument had a rain shield placed 12cm above it and a 1 in. mesh screen around it as protection against marauding animals. To assure equivalence in the records, the instruments were operated together for at least 12 hours before each test.

Representative terrain situations tested on various parts of the island included a *clearing* and a *forested plateau*, a *ridge top* and a *ravine bottom*, a *north-facing slope* and a *south-facing slope*. In addition three former bivouac sites, two statary and one nomadic, were tested. In these latter tests one instrument occupied the former bivouac site and the control instrument was placed five meters away on the same contour. Results are summarized in Table 6.

The daily marches of relative humidity and temperature show great regularity from day to day. The temperature was highest from 12 to 3 P.M. each day and lowest from 5 to 7 A.M. with little variation. The average daily maximum temperature from 40 daily records on the forest floor was $28.3 \pm 1.6^\circ \text{C}$. The average daily minimum was $21.9 \pm 1.1^\circ \text{C}$. Relative humidity regularly showed a steady rise from a low around 2 P.M. to a high around 9 A.M. It characteristically showed a sharp drop across midday. The average daily maximum from 40 records was $93.4 \pm 1.4\%$, and the average daily minimum was $71.2 \pm 7.4\%$.

TABLE 6. Five-day averages in temperature and relative humidity for three series of contrasting sites—dry-season records: February, 1948. (Both members of each series run concurrently.)

Terrain	TEMPERATURE (°C.)			RELATIVE HUMIDITY (%)		
	Maximum	Minimum	Range	Maximum	Minimum	Range
1. Ridge top.....	27.5	20.6	6.9	95.0	61.5	33.5
Ravine.....	26.1	19.2	6.9	94.5	82.0	12.5
2. North Slope.....	33.3	20.6	12.7	94.5	55.5	39.0
(Windward)						
South Slope.....	31.1	20.0	11.1	95.5	63.0	32.5
(Leeward)						
3. Forested plateau...	28.0	21.9	6.1	94.0	72.0	22.0
Clearing.....	28.9	22.9	6.1	87.5	63.0	24.0

In the forest the greatest fluctuations in temperature and relative humidity occur during the dry season, when these records were taken. If extremes in either of the two atmospheric conditions were to affect the Ecitons, the dry season would be the more critical. As might be expected, a very irregular terrain on the island contributes materially to variations in local microclimates. The averages for various types of terrain investigated in the dry season are shown in Table 6.

The table indicates little variation in temperature among the various types of terrain but shows a marked difference in the range of relative humidity. Eciton bivouacs on ridge tops and windward slopes would be subject to considerably more desiccation than those in ravine bottoms. This desiccating effect would appear to be related to the degree of exposure to the prevailing northeasterly winds so characteristic of the dry season in this area. Little difference is shown between locations in the clearing and forest (Series 3) when both spots are sheltered from the wind.

Variations in the microclimate at different times of day also may have some bearing on Eciton activities. At the time in the dry season when these records were taken the greatest differences in temperature near the forest floor occurred shortly after midday when differences of as much as 4-11° C were recorded. On the other hand, differences of the smallest magnitudes were found at dusk and dawn. The least differences from place to place were found between 7:00 and 10:00 P.M. when the range of variations fell between 0.5 and 1.2° C. The greatest range in relative humidity near the forest floor almost always occurred in the early afternoon between 1:00 and 2:00 P.M. The average relative humidity from 80 records taken during this period was $73.8 \pm 7.9\%$; the range was 31.5%. Relative humidity showed its smallest variations throughout the forest during the night and very early morning. The average of 120 records taken between 7:00 and 10:00 P.M. was $86.4 \pm 3.0\%$; the range was 14.0%. Between 7:00 and 8:00 A.M., when the daily relative

humidity is highest, the average of 80 readings was $83.0 \pm 1.5\%$ with a range of 7.5%.

The general uniformity in relative humidity and in temperature which prevails at night from area to area throughout the forest may be very important to the developing larval brood. The emigrations of these terrestrial Eciton species occur in the evening and night, and most frequently the larval brood is transported from bivouac to bivouac between the hours of 7:00 to 10:00 P.M. As a rule, therefore, the larval brood is exposed to the conditions of the general forest atmosphere only during that time when humidity and temperature tend to be equable and nearly uniform throughout the general habitat.

Unfortunately it was possible to investigate only the few former bivouac sites which could directly accommodate the bulky instruments without altering the site. The test bivouac sites were: 1) a former *burchelli* bivouac site of the nomadic phase, near the border of a fallen-tree clearing under good upper forest cover, with the control instrument under much the same cover but on relatively open forest floor; 2) a former statary site used by colony '46 B-I (*E. burchelli*) from February 7 to 27, 1946, under good forest cover within a tree cavity at a point about 2.8m from the ground (directly open to the outside on the western or downhill side through a hole about 45cm high and 25cm wide), with the control instrument under good upper cover on the open hillside; 3) a former statary site occupied by colony '48 H-12 (*E. hamatum*) from December 7 to 27, 1947, under good upper forest cover in an open area on a southern hillside exposure, within the hollow of a large log shell about one meter from the open end. Both the log site and the control location were in a small natural clearing on a hillside gently sloping toward the south. A summary of the results is presented in Table 7.

With respect to the tree-mass nomadic site, the diurnal maximum for temperature is somewhat deceptive, for actually the temperature of this spot rose above that of the control point only for about one hour each midday, when the brush mass was reached by direct sunlight through a gap in the tree canopy. Otherwise, the daytime temperature of the former nomadic site characteristically fell

TABLE 7. Five-day continuous hygrothermograph records from three bivouac sites and their controls.

Site	% RELATIVE HUMIDITY			TEMPERATURE		
	Av. daily minimum	Av. daily maximum	Av. daily range	Av. daily minimum	Av. daily maximum	Av. daily range
Tree mass.....	63.0	89.5	26.5	21.7	31.7	10.0
Control.....	58.6	95.5	36.5	21.7	29.7	8.0
Log hollow.....	75.5	91.5	16.0	23.1	26.9	3.8
Control.....	66.5	95.0	28.5	22.8	29.4	6.6
Tree hollow.....	66.0	88.1	22.1	22.5	24.4	1.9
Control.....	62.6	93.0	30.0	22.2	31.4	9.2

below that of the control area and the nighttime temperature tended to be somewhat higher. As a smaller range in relative humidity suggests, the bivouac spot tended to be more humid in the daytime and somewhat drier at night than the control location.

The results for the two investigated statary sites indicate that both tended to be definitely warmer during the night and cooler during the day than the controls, *i.e.*, both exhibited considerably lower ranges of variation in temperature than the controls. Both statary bivouac sites also were markedly less variable in relative humidity than were their controls.

In the original tracings, it is noticeable that for the greater part of the five-day interval in which records were made at the hollow-tree statary site, so limited are the fluctuations in both temperature and humidity lines that the diurnal character of the records disappears almost completely. In contrast, it is pronounced for each day in records from nearby more exposed sites used as controls.

EFFECT OF DESICCATION ON ECITON ACTIVITY AND SURVIVAL

The most radically fluctuating atmospheric condition during the dry season appears to be humidity. It is very possible that this factor might well be the most critical of all atmospheric conditions involved in the adjustive relations of Ecitons to their environment. Such a possibility has been strongly suggested by the occasional discovery, in exposed areas at especially dry times, of army-ant colonies notably reduced in size and with a disproportionately high number of major workers (Schneirla 1949b; Schneirla & Brown 1950). Over a period of years, cases of this kind have arisen sufficiently often to suggest that the various castes may be differentially susceptible to some reductive environmental condition with lethal effects at its extremes. In tests designed to clarify the nature of this reductive effect, the most specific results were obtained with a homogeneous behavior situation in which workers of *E. hamatum*, in the caste proportions normal to a functioning colony, were subjected to a progressive desiccation.

A most satisfactory behavior situation, from the standpoint of relative uniformity of function in all participants, was found in the circular columns which are readily established in groups of Eciton workers segregated with larval brood in laboratory nests (Schneirla 1944b). In the experiment to be described, two groups of *hamatum* workers, containing about 200 individuals each, were established in separate metal pans (4 x 8 x 3 in. deep), and the test was begun when both groups had established their circular columns around a central obstruction. Relative humidity was recorded from wet- and dry-bulb thermometers inserted through holes in the side of each pan near its center.

When experimental and control columns were well developed, anhydrous calcium sulfate was added to

containers in the experimental area. The record in Table 8 shows that the atmosphere in the experimental pan then was subject to a rapid reduction in relative humidity. Within two hours relative humidity had fallen to 50%, and thereafter remained near or below this value. Throughout, the air in the control pan was maintained near saturation. Readings of the wet and dry bulbs were taken every ten minutes, as well as records of the speed, behavior and general condition of ants in the two columns. In Table 8 below, in which is given a general report on concurrent conditions in relative humidity and in condition of the two groups of ants, the times represented are those at which major changes were recorded in the condition of the experimental group.

The results were clear-cut. Under relatively stable atmospheric conditions with humidity held near maximum, the control group retained its group function in a vigorous and essentially uniform condition. The experimental group, at the outset equivalent in condition to the control group, soon showed a progressively worsening behavior and function, and after about five hours all of its members were dead. The minor worker castes were first to be affected in function and first to die, the intermediates next, the sub-majors and majors last of all.

TABLE 8. Influence of relative humidity upon the function of Eciton workers in a specific activity pattern of relatively uniform character.

Time of observation (P.M.)	RELATIVE HUMIDITY (%)		BEHAVIOR AND CONDITION OF GROUPS	
	Experimental chamber	Control chamber	Experimental	Control
1:50....	95.5	99.3	Vigorous	Vigorous
2:30....	76.0	98.0	Decreased vigor	Vigorous
3:30....	50.0	98.0	Small cluster of workers on wet bulb	Vigorous
4:00....	47.1	99.2	Speed about same as control, but column now variable and "poorly organized"	Vigorous
4:45....	43.5	98.8	Now shows "severe deterioration," with many minor workers lying on their sides	Vigorous
5:15....	52.5	99.2	Column slow and "poor," with minor and intermediate workers mostly dead or dying	Vigorous
5:30....	47.4	98.9	Column formation largely gone	Vigorous
6:00....	50.6	100	Column very slow and erratic; only major workers remain, and they are shaky and erratic in movement	Vigorous
10:15....	73.9	100	No column; no ants on feet, no motion except in majors and larger intermediates, which show only leg reflexes	Slower (under Mazda light), but still large and moving smoothly

It is evident that under natural conditions Eciton colonies may suffer population losses through a sustained lowering of atmospheric humidity toward the lethal point. In our experimental area, relative humidity fell rapidly from near saturation to a low point near 50% which was maintained after two hours. The lethal point for all Eciton castes evidently lies somewhere below 60% R.H. The lowest relative humidity we have recorded in the forest was taken on a windward slope and for a time remained at 55.5%. There are places in the forest such as fallen-tree areas, reached for longer times by full sunlight, in which Eciton colonies might be subject to extreme desiccation over long intervals or by repeated exposure. Under such conditions, a colony might suffer considerably, especially in its less resistant minor and intermediate castes. The possibility should not be excluded that temperatures above a given tolerance level may exert comparable effects (Wigglesworth 1939; Schneirla 1949b; Roeder 1952).

THE MICROCLIMATE WITHIN THE BIVOUAC

It has been shown that the general environment of terrestrial Ecitons is very constant, especially as far as temperature is concerned. Under forest conditions, the humidity factor appears to be more variable and more critical as concerns possible crises. It remains to be seen how well Eciton colonies are able to maintain an intra-bivouac microclimate and how great an influence is exerted on the internal environment of the bivouac by changes in the external atmosphere.

Because temperature is well-established as a controlling factor in insect development (Wigglesworth 1939; Roeder 1952) and because of expediency, temperature records were sought as our best means of evaluating the intra-bivouac microclimate. In studies with particular colonies, temperature data were recorded from various locations within the bivouac proper, and during various parts of the nomadic-statory cycle. For comparison, each intra-bivouac reading was matched with temperatures taken concurrently in the nearby external environment. The instruments used were immersion-type mercury-in-glass thermometers accurate to within at least 0.5° C. In each reading, the thermometer was held in place at the test spot, inside or outside the bivouac, until the mercury level became stabilized. This usually required about three minutes.

Diurnal atmospheric changes within the bivouac. In Figure 5 are shown the results of temperature measurements taken at half-hour intervals for several consecutive hours at each of three different bivouac locations of *E. hamatum*. Also, a section of data from a statory bivouac of *E. hamatum* is presented in Table 9.

These data suggest that in the daytime the internal temperatures of both nomadic and statory bivouacs are maintained at a level above that of the atmosphere surrounding the bivouac. In these series of readings, temperatures within the bivouac almost without exception exceed extra-bivouac control readings by

TABLE 9. Diurnal variations in intra- and extra-bivouac temperatures at a statory bivouac site of *E. hamatum* (colony '48 H-1).

Date	Time of day	TEMPERATURE READINGS IN °C.				
		Intra-bivouac			Extra-bivouac	
		Top center	Bottom center	3-5 cm. off at top level	1 meter off at top level	3 meters off, ground level
11/22/47.....	9:15 a.m.	27.2	27.2	25.2	26.1	26.1
11/23/47.....	10:30 a.m.	27.0	26.8	27.0	26.5	25.0
11/24/47.....	12:00 p.m.	27.5	27.5	26.8	26.0
11/29/47.....	12:00 p.m.	27.2	27.0	24.0
11/22/47.....	7:30 p.m.	27.0	26.5	26.0	25.5	25.5
11/23/47.....	7:45 p.m.	27.0	27.0	25.5	24.8	25.0
11/24/47.....	7:45 p.m.	27.0	27.0	25.5
12/2/47.....	7:05 p.m.	26.9	25.9	23.3	22.5	22.4
Range of daily readings.....		0.6	1.6	3.7	4.0	3.7
Average.....		27.0	26.9	25.3	25.1	25.0
Average Deviation.....		0.2	0.3	1.0	1.2	0.9

1-2° C or more. In the case represented in Table 9, although an average temperature near 27° C held within the bivouac at different times of day, extra-bivouac temperatures averaged near 25° C. Furthermore, intra-bivouac temperatures were less variable, with an Average Deviation of only 0.2-0.3° C in contrast to 0.9° C or more for extra-bivouac temperatures at corresponding times of day.

The great constancy found in bivouac temperatures at different times of day in the statory phase, as represented in Fig. 5-A, suggests that under these conditions the environment inside the cluster is more independent of environmental changes than are the temperatures within nomadic bivouacs.

A relative independence from the external atmosphere so far as temperature level is concerned may be considered a characteristic of nomadic bivouacs as well. It will be seen in Figs. 5B and 5C that the variation in temperature at locations within the bivouac is appreciably less than that at locations outside the bivouac. This point is illustrated strikingly in the case represented in Fig. 5C, in which a continuous rain was effective throughout the record-taking. Clearly as a result of this, there was a considerable and protracted fall in temperature in the outer atmosphere. Within an interval of more than six hours of rather steady rain, although extra-bivouac temperatures fell through about 4° C, temperatures close to the brood area within the bivouac fell through only about 1.7° C. Moreover, it will be noted that in contrast to a relatively sudden fall of about 3° C in external temperature within one hour after the rain began, intra-bivouac temperatures exhibit a definite latency in beginning a fall which carried only through about 1° C in the same interval.

Bivouac microclimate through the cycle. Numerous conditions oppose reliable measurements of intra-bivouac conditions in the same colonies over considerable periods of time. The nomadic bivouacs of successive days usually differ considerably in their form, accessibility, and internal makeup, and statory

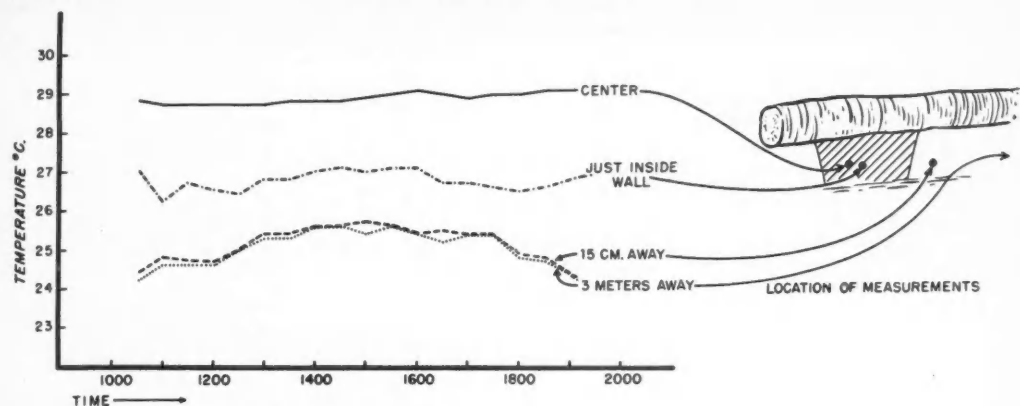
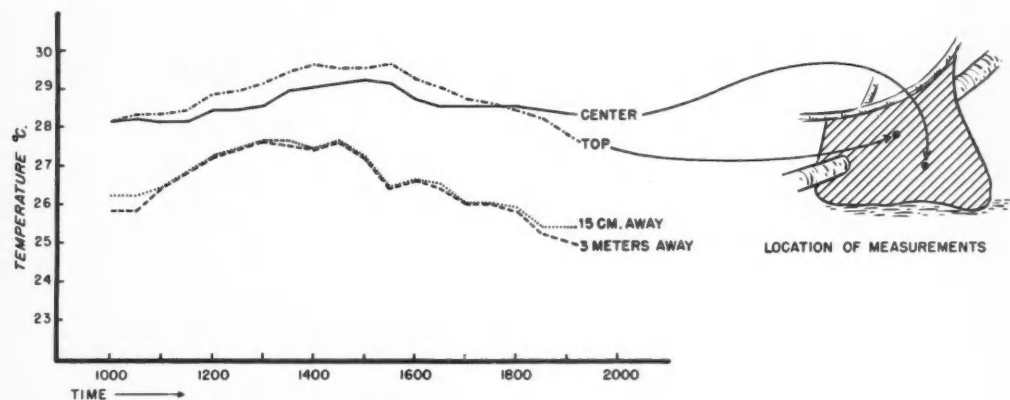
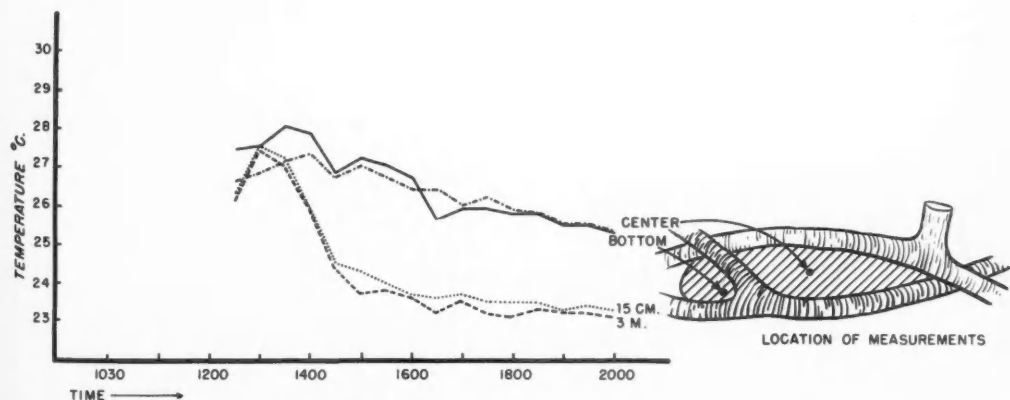
A. COLONY '49 H-34, 4th STATARY DAYB. COLONY '49 H-34, 16th NOMADIC DAYC. COLONY '49 H-33, 3rd NOMADIC DAY

FIG. 5. Intra-bivouac temperature readings with corresponding extra-bivouac control readings taken at 30-minute intervals through the day in the early statary (A), the late nomadic (B) and the early nomadic (C) phases in two colonies of *Eciton hamatum* (September, 1949—rainy season).

In each case, the two intra-bivouac locations which were approached as closely as possible with the mercury in successive readings are indicated in the corresponding lateral sketch of the bivouac at the right, and the records are given in the two upper curves with the extra-bivouac control records in the two lower curves. The record closer to the intra-bivouac center is indicated in each case by the solid line; that from the more peripheral location by the broken line above—the records from the extra-bivouac control locations are indicated by the broken lines running well below. In C, rain fell more or less continuously from shortly after 1:30 P.M. (1330) to 8:00 P.M. (2000).

bivouacs often approach or attain a virtual inaccessibility, particularly in the intermediate part of the phase. Progressive changes in form and internal pattern may be paramount in importance, as is indicated by evidence cited in section 5 concerning variations in spatial distribution of the brood according to developmental stage. There also occur variations in the mass centering of the brood in the bivouac according to the physical character of the bivouac situation, particularly with respect to support and cover.

Intra-bivouac temperatures were recorded by the junior authors throughout both phases of a cycle in two colonies in the rainy season of 1949. The data in Table 10 are summarized from the nomadic phase of one of these colonies. Each day the measurements were made as close as possible to 10:00 A.M. This evidence suggests that the temperature inside the bivouac is consistently higher and undergoes less variation than that of the surroundings throughout the entire range of the nomadic phase.

TABLE 10. Bivouac temperatures ($^{\circ}$ C.) at 10:00 a.m. through a nomadic phase (colony '49 H-34, *E. hamatum*).

	INTRA-BIVOAC TEMPERATURES		EXTRA-BIVOAC TEMPERATURES	
	Readings in top half of bivouac	Readings in bottom half of bivouac	Readings at top level, 15 cm. from bivouac	Readings at top level, 3 meters from bivouac
Average.....	27.77*	27.47	25.67	25.66
Number of readings....	N=63	N=61	N=18	N=16
Standard deviation.....	0.485*	0.654	0.645	0.695

*For the upper third of the bivouac, the average is 27.6° C., the S.D., 0.25° C.

At this time in mid-morning bivouac temperatures were consistently higher by nearly 2° C than were atmospheric temperatures in the nearby outer environment. Furthermore, for this time of day bivouac temperatures tended to be less variable from day to day than external temperatures, as indicated by a smaller Standard Deviation for top intra-bivouac temperatures than for outside temperatures during the phase.

It is important to specify the specific locations where temperature records are taken within the bivouac. This is especially true of nomadic bivouacs, in which bivouac sites are changing daily. In the readings for nomadic bivouacs taken daily at 10:00 a.m. (Tables 10, 12), the top center and bottom center of the cluster were involved. Much the same average temperatures prevail for these two localities under the conditions stated. However, variability is less for the upper center, as is indicated by a Standard Deviation of 0.485 for the upper half as against 0.654 for the bottom half. Even less variable was the upper central third, with a Standard Deviation of 0.25° C for the phase. The early larval brood is generally posted in the upper center of the bivouac, and the smallest members of the brood tend to be

clustered in this locality throughout the phase. The data in Table 9 indicate that in a statary bivouac as well, top center has less variation in diurnal temperature than has bottom center.

Results from these same two colonies studied in the rainy season of 1949 are graphed in Figure 6. These findings indicate a high stability throughout the statary phase as well, notwithstanding a considerable diurnal fluctuation in the general environment. In '49 H-34, for example, we note that in 47 measures, all but the lowest five intra-bivouac readings lie between 27.8° and 29.9° C, i.e., within a range of 2.1° C, in contrast to a range of concurrent extra-bivouac readings between 23.8° and 26.6° C. The lowest intra-bivouac temperatures were nearly always above the highest extra-bivouac temperatures. In the statary phase, intra-bivouac temperatures are distinctly higher than extra-bivouac temperatures.

Not only were intra-bivouac temperatures found distinct from those in the general environment and strikingly stable through the day, but this condition of internal stability prevailed throughout the statary phase despite a considerable extra-bivouac fluctuation. In the statary phase records of H-34, for example, extra-bivouac temperatures rose to a peak at the 13th day, but this notable rise was not paralleled within the bivouac. A distinct fall in extra-bivouac temperatures in the last five days of this phase was not duplicated within the bivouac; instead, actually higher internal temperatures were recorded than earlier in the phase. In the case of colony '49 H-33, in contrast, extra-bivouac temperatures reached and maintained their highest level during the last few days of the statary phase, but without any demonstrable effect on the situation within the bivouac.

Table 11 offers a useful summary of the two cases presented in Fig. 6, to show what relationships prevail between the internal and external temperatures of the bivouacs of *E. hamatum* through the cycle. The averages, all reliably different, indicate that intra-bivouac temperatures were consistently higher than extra-bivouac temperatures throughout both nomadic and statary phases.

Intra-bivouac temperatures are not maintained on the same level in the two phases. As Table 12 shows, in the statary phase of H-34, 82% of 47 readings are between 28 and 30° and 4% are below 27° C, whereas in the nomadic phase only 35% or 44 of 128 readings are in the $28-30^{\circ}$ range and 19% are below 27° C. (Table 11). In the statary phase of H-33, 71% or 58 of 81 readings are between 28 and 30° C, with only 5 (or 6%) below 27° C, whereas in a succession of nine nomadic days 43% or 25 of 59 readings are in the $28-30^{\circ}$ C range and 34% are below 27° . At the time of day measurements were taken regularly, in mid-morning, a higher level of intra-bivouac temperatures prevailed in the nomadic phase than in the statary phase.

Variations occur in the intra-bivouac microclimate, recognizably in relation to colony condition. The

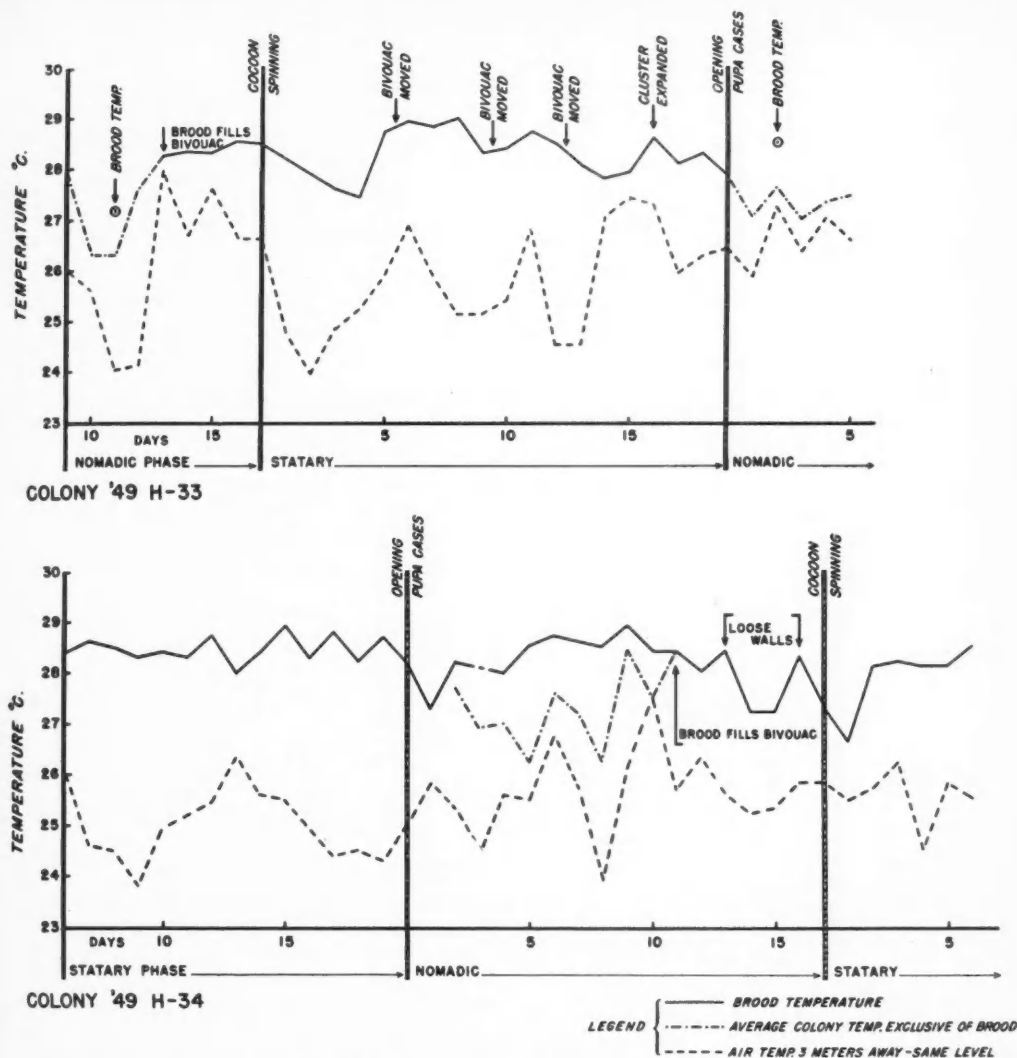


FIG. 6. Records of intra-bivouac temperatures taken near 10:00 A.M. daily through an activity cycle for two colonies of *E. hamatum*, in comparison with control air temperature readings taken at 3 meters from the bivouac. Each record is an average of 4-6 readings. In the record of colony '49 H-33, brood temperature is represented separately in two exceptional instances in which the thermometer penetrated to the center of the larval-brood mass.

lowest intra-bivouac temperatures of the statory phase were recorded on the first two days (Fig. 5), when spinning continues and the structure of the bivouac wall is loose.

With the narrow exception of the last section of the phase in colony H-34, smaller Standard Deviations are found for intra-bivouac as against extra-bivouac temperatures in the successive thirds of the statory phase in both colonies (Table 10). This may be taken as an indication of the great stability of the internal bivouac environment during the statory phase. In contrast, higher S.D. values for

intra-bivouac temperatures in the nomadic phase indicate that internal conditions are more variable through this phase. It must be kept in mind that a more variable internal bivouac situation in the nomadic phase nevertheless has distinct characteristics of stability in that thermal conditions are maintained at a level above those of the external environment.

In the nomadic phase of colony H-34, as Table 13 indicates, lower temperatures were recorded for the early and late stages than in the intermediate part of the phase. For days 2-5, 25 of 30 readings (or

TABLE 11. Average temperatures for nomadic and statary phases in two colonies of *E. hamatum*.

A. Colony '49 H-33										
Location	Nomadic				Statory				Nomadic	
	Days 9-17		Days 1-4		Days 5-15		Days 16-19		Days 1-5	
	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.
Intra-bivouac.....	27.3	0.6	27.8	0.3	28.5	0.4	28.3	0.3	27.3	0.33
Extra-bivouac.....	25.8	1.88	24.8	0.38	25.7	0.76	26.2	0.42	26.4	0.55

B. Colony '49 H-34													
Location	Statory						Nomadic						Statory
	Day 6-9		Day 10-16		Day 17-20		Day 2-5		Day 6-13		Day 14-17		Day 1-6
	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.	Ave.	S.D.	Ave.
Intra-bivouac.....	29.5	0.12	28.4	0.27	28.3	0.5	27.7	0.92	28.0	0.38	27.9	0.70	28.0
Extra-bivouac.....	24.6	0.67	25.6	0.43	24.6	0.3	25.2	0.36	25.9	0.81	25.9	0.33	25.7

TABLE 12. Intra-bivouac temperatures for two colonies of *E. hamatum* according to phase.

Temperature interval	STATARY PHASE				NOMADIC PHASE			
	H - 34		H - 33		H - 34		H - 33	
	Cases	%	Cases	%	Cases	%	Cases	%
Above 29° C....	9	19	14	17	7	5	1	2
28-29.9.....	30	63	44	54	37	29	24	41
27-27.9.....	4	9	18	22	59	45	14	24
26-26.9.....	4	9	4	5	22	17	14	24
25-25.9.....	0	0	1	1	3	2	6	10
Total.....	47	..	81	..	128	..	59	..
Above 28°	82	..	71	..	34	..	43

83%) and for days 14-17, 25 of 31 readings (or 81%) fell below 28° C, in comparison with 34 in 66 readings or 51% in the intermediate part of the phase. The lower temperatures seem related to a looser structure of the bivouac wall, attributable in the first few days to the presence of callows and in the last few days to spinning activities in the mature larval brood. Relatively few readings above 28° C were obtained in the first and the last few days of

the nomadic phase, presumably because brood center (where temperatures are highest) was then very difficult to locate.

DISCUSSION

In the behavior and biology of the terrestrial army ants, a highly regular and resilient system of adaptive resources prevails (Schneirla 1949a). Colonies of these neotropical ants are restricted almost exclusively to the forests, which through long geologic time have afforded the relatively stable conditions presumably essential for the evolution of their intricate adaptive system. A long-term continuance of stable forest conditions would seem indispensable for the rise and persistence of a pattern insuring an optimal terrestrial microclimate despite regular shifts in nesting site. In the tropical forest environment of terrestrial *Eciton* species, variations in atmospheric conditions fall within a narrower range than that prevailing in biotic areas such as the tropical savannahs and the Temperate Zones into which species in the subgenus *Neivamyrmex* have spread successfully. A more precise adaptive pattern is thereby suggested in the former.

The ecological niches occupied by *Eciton* species in neotropical forests range in vertical level from that of species such as *E. (Eciton) burchelli* which are terrestrial and even arboreal to that of almost completely subterranean species such as *E. (Labidus) coecum*. The terrestrial nesting tendency is strong only in the two species studied in this investigation, and in them is accompanied by an equally predominant terrestrial tendency in raiding; whereas in the numerous remaining species the subterranean nesting tendency runs progressively stronger to an extreme, roughly paralleled by a subterranean raiding tendency in the respective species. Von Ihering's (1912) suggestion that a subterranean way of life must have evolved in *Eciton* under savannah con-

TABLE 13. Nomadic-phase temperatures for colony '49 H-34 (*E. hamatum*).

Temperature range	INTERVAL IN PHASE					
	Days 2-5		Days 6-13		Days 14-17	
	Cases	%	Cases	%	Cases	%
Above 29°.....	1	3	6	9	0	0
28-28.9.....	4	13	26	39	6	19
27-27.9.....	11	37	27	40	21	68
26-26.9.....	11	37	7	10	4	13
25-25.9.....	3	9	0	0	0	0
Total.....	30	..	66	..	31	..

ditions implies that continuous deep-forest conditions must have been available for the emergence and continuance of the terrestrial species of the New World. From this one might think that in the Old World tropics, in which no strongly terrestrial doryline species exist, the conditions of evolution evidently involved a historical discontinuity of deep-forest conditions. A study of conditions and variations in the typical microclimate of terrestrial *Eciton* species proves of interest in the light of such questions.

Like the nests of most social insects (Emerson 1938), the nests of terrestrial *Eciton* species vary in their microclimatic properties in relation to the daily rhythm of extrinsic conditions. But in all social insects, to relatively different extents, there is an appreciable degree of inertia in the response of the nest microclimate to external changes, and conditions seldom reach the extremes of the outer environment even in cases of the poorest internal regulation. In all social insects, that is, the nest not only affords a shelter for population and brood but also serves to smooth out somewhat the variations of the outer environment (Allee *et al.* 1949). Although the *Eciton* bivouac is not fixed or permanent but is re-established periodically in different localities, our evidence indicates that it is one of the most efficient sheltering systems among social insects.

The temporary nest, particularly in its role of brood incubator, is a key factor in the *Eciton* adaptive pattern. This is indicated by the year-around regularity of the nomad-statory cycle in the terrestrial species, with predictable phase durations characteristic of the species (Schneirla 1946; Schneirla & Brown 1950). It is a well-established fact that, in general, insect developmental metabolism is delicately attuned to atmospheric conditions such as temperature and humidity (Uvarov 1931; Buxton 1932; Wigglesworth 1939; Ryan 1941; Ludwig & Anderson 1942; Davidson 1944; Ludwig 1945; Pradhan 1946; and Browning 1952). In view of this fact, the prevalence of a relatively high precision in the duration and recurrence of *Eciton* activity phases speaks for a stable set of microclimatic conditions for the brood at all stages. In keeping with this expectation, we have found the bivouac essentially a constant-temperature brood chamber in the statory phase and an adjustable brood-chamber of relatively stable properties in the nomadic phase. This condition holds despite the transient nature of both types of nest with the bivouac reconstituted at a new site each day in the nomadic phase, when the brood completes its larval stage of development.

Terrestrial *Eciton* colonies present an intriguing problem in habitat selection, as they are capable of changing their nesting locales with far greater regularity and probably greater frequency than any other social insect. With roughly ten nomad-statory cycles in a year, a colony of *Eciton hamatum* can occupy a total of about 170 different nesting sites; that is, about 160 relatively exposed nomadic sites

and 10 relatively enclosed statory sites. Our findings (Sections 2 and 3) indicate that numerous and varied factors relating to behavior operate against the mischance of any colony occupying and remaining in a non-optimal spot.

The successful survival of colonies notwithstanding their persistent shifting about in the general environment indicates that a "selection" process of some kind favors the taking of ecologically optimal sites. Even the open sites of the nomadic phase generally have atmospheric properties more favorable to the clustered *Eciton* colony than have alternative spots in the general environment (Sections 1 and 6). It seems inconceivable that the occupied sites with their more propitious qualities could be hit upon in a purely random fashion. However, if a systematic process is involved its nature is not readily discernible. Conceivably, a colony might select new sites through the discriminative responses of workers to local environmental differences in clustering operations after nightfall. On its face, the hypothesis of a direct discriminative process in bivouac establishment seems reasonable. Favoring this idea is the probability that *Eciton* workers share the relatively delicate sensitivity to environmental differences in temperature and humidity common to social insects (Herter 1924, 1925; Kennedy 1927; Himmer 1932; Gösswald 1938, 1948, 1941; Marcus 1948; Gebhardt 1953) and presumably are sufficiently acute in these modalities to be affected by prevalent diurnal differences between the atmosphere of the bivouac site and nearby locations.

However, we are strongly inclined to discard this hypothesis, not only because no direct evidence for it has arisen in our studies of bivouac establishment, but also on circumstantial grounds. Against it stands the fact that in the early evening and night, during the very period when the eventual bivouac site is generally hit upon and alternatives are eliminated, atmospheric conditions tend to be uniform throughout the general environment of the tropical forest, more nearly alike than at any other time around the clock. In other words, locations at which extremes of temperature, dryness, or light would prevail in the daytime are all likely to be closely similar in their evening properties, and to approximate the species optimum. Therefore, a selection of potential sites by terrestrial *Ecitons* on the basis of atmospheric conditions would seem improbable. Yet the fact remains that the atmospheric properties of bivouac sites typically fall closer to the evident species optimum than do those of control locations nearby.

Our evidence indicates an *indirect* type of selection process in the localization of *Eciton* nomadic bivouacs. First of all, because *Eciton* colonies generally establish their bivouacs on or near the chemical trails formed and used in the daytime raid (Schneirla 1933, 1938, 1949b) worker responses in the initial formation and continued use of raiding trails would seem of some consequence for eventual bivouac placement, however devious the connection might be. Thus, in

the terrestrial species, the likelihood of relocating at the day's end in a place beyond the forest edge or under sparse cover is reduced by the common tendency of workers in the daytime raid to avoid intense sunlight in their advances into new terrain. Eciton bivouacs tend to be established at or close to the junction points of former raiding trails, and although optimal bivouac conditions might not seem to follow from this fact, such is often the case. Trail-division points are unlikely to become or remain the sites of booty-cache formation during the afternoon if the locality is disturbingly bright, hot or dry. Thus many non-optimal zones may be eliminated as potential bivouac sites long before the initial stages of bivouac-clustering begin.

Also, once the specific clustering starts at some time after dusk, it does not ordinarily proceed very far as a rule in places where hanging strands cannot form readily. This favors places with good ceilings—spaces beneath raised logs, the root interspaces of trees, vine masses and the like. Such places happen also to be the ones likely to provide an appreciable amount of cover on the following day. When this is not the case, and next day the colony becomes over-exposed to disturbing environmental conditions, secondary behavioral readjustments of limited scope are still possible.

Terrestrial Eciton colonies attain their best shelter and most stable microclimate in the statary phase, when delicate and rather precarious processes are accomplished such as pupation in the advanced brood, physogastry and egg-laying in the queen, and hatching of the eggs. The hypothesis of a direct discriminative selection, discarded for nomadic sites, might seem applicable to colonies entering the statary phase, when physically sheltered places such as hollow logs are entered rather than open places. Such places are distinguished in their atmospheric properties as uniformly cooler and more humid than open nomadic sites. Moreover in the dry season, when the general environment presents its greatest extremes of the year, colonies of both *E. hamatum* and *E. burckellii* take well sheltered sites more frequently than in the rainy season.

The tendency of terrestrial Eciton colonies to enter enclosed places when the larval brood is mature presents the most difficult habitat-selection problem of the cycle. Although, as we have found, the ecological properties of the statary microclimate are distinct and more stable than those of the nomadic, no evidence is at hand to indicate that these more sheltered places are entered through direct discriminative responses by workers to atmospheric differences. Also puzzling is the fact that places such as hollow trees and mammal burrows are often entered in the last few nomadic days, while the larval brood is in the early stages of spinning, and before the statary phase proper.

To explain the acquisition of statary sites it seems necessary to adopt as a basis the processes underlying the selection of nomadic sites, but also to postulate new factors. Our evidence shows that al-

though emigrating colonies always tend to begin open clusters regardless of condition, when a mature larval brood is present the process of resettlement is protracted by behavioral complications. Events now are more time-consuming, since many and various open clusters form and disappear before any enclosed site is entered. These circumstances indicate a selective process more involved than that in the formation of a nomadic bivouac.

Our best clue seems to lie in the level of excitability of the adult worker population at different times in the nomadic phase. A difference in this respect between the late and earlier stages of this phase is indicated by a simple test carried out with hanging strands forming in open places. Gently blowing on these strands always disturbs the clustered workers and causes the strands to break down to some extent. Earlier in the phase the disturbance tends to be partial and short-lived, and a repetition of the test even at short intervals usually does not stop clustering unless extreme measures are adopted. But late in the phase, the outcome is different. A similar intrusion now produces a more radical and lasting disturbance among the first strands at a clustering point, and the process of bivouac formation may be blocked altogether. With the larval brood close to maturity, the workers are disturbed with exceptional ease in activities such as clustering.

For the worker population of a colony nearing the end of the nomadic phase, an unusually low threshold of excitability may be postulated, admitting a condition of hyper-irritability as an organic "set" which increases as the brood nears its peak of maturity but which drops sharply away as the larval brood becomes mainly enclosed. While this condition persists, bivouac formation during emigration involves far more than the ordinary number of interruptions. Then new strands or even larger clusters tend to dissipate at relatively slight environmental disturbances; minor intrusions may produce a widespread collapse even in established bivouac clusters. Under this handicap, clusters are unlikely to continue far toward completion in exposed places. A typical source of such effects is the brisk air currents which commonly arise in the forest during evening hours and which are especially strong in the more open forest of the dry season with the Trade Winds in force.

At such times, bivouac establishment is a variable and time-consuming process as a rule, with several clusters begun in open places before a well sheltered place is hit upon and the operation completed. During most of the nomadic phase, workers engaging in the first section of an emigration generally reach an advanced stage in consolidating one of their first exposed clusters within two or three hours after dusk. But near the end of the phase, colonies frequently do not settle upon a bivouacking place until well after midnight.

A further hypothesis concerns the tendency of workers carrying mature larvae to deposit them in places where wood detritus and similar material

abounds, hence in enclosed places. This may be a contributing factor, at least, to the nature of the statary bivouac.

Notwithstanding their success in getting into optimal sites, Eciton colonies occasionally occupy very unsuitable habitats. In such cases, an appreciable measure of readjustment can come about through the active responses of workers to extremes of temperature, dryness, and light. A local disturbance of the bivouac, as by a sun fleck, if sufficiently lasting, may cause shifting from the affected zone and repatterning of the cluster. Such disturbances lead to a stimulative summation and soon thereby to widespread responses of the colony, so that as a sequel the entire cluster may be relocated. Thus, colonies which chance to bivouac in places where they are unprotected by forest canopy, as in a fallen-tree zone or even beyond the edge of the forest, may escape the lethal effects of solar radiation or at least reduce the hazard appreciably. The survival of a terrestrial nomadism in these Ecitons must have been aided greatly by the fact that the bivouac has dynamic properties which make it an adjustable sheltering device.

Between the two species studied, some differences have been found in bivouacking, against the background of a fundamentally similar pattern. The principal difference is a much greater arboreal nesting tendency in *burchelli* than in *hamatum*. At present, the basis is not entirely clear. The distinction may be due on the one hand to species differences in sensitivity to atmospheric conditions, and indeed an appreciable altitudinal gradient both in temperature and in humidity is common in neotropical forests (Allee 1926a; Richards 1952). On the other hand, it may be a subtle by-product of secondary behavioral differences, somewhat as we have suggested for the "selection" of terrestrial sites. Thus, *burchelli* generally forages in the forest vegetation at all strata and even high in the trees in greater and more concentrated numbers than does *hamatum*, which would favor a post-raiding formation of clusters in elevated places in the former species. Clusters are much more likely to continue and persist if large numbers of workers are soon at hand once the critical early stages of strand-formation have begun. This condition holds especially late in the nomadic phase, at the peak of raiding, when elevated statary bivouacs are common in *burchelli*. On the rare occasions when *hamatum* establishes such elevated bivouacs, these structures are formed by large colonies as sequels to unusually populous raids, or by colonies in the excitable condition of the late nomadic phase.

Although Eciton bivouacs are only transient erections they serve as very efficient brood incubators. Eciton broods, like those of insects generally (Wigglesworth 1939; Ludwig & Anderson 1942; Davidson 1944; Pradhan 1946; Browning 1952; Roeder 1952) are delicately responsive in their metabolism to the atmospheric conditions of the environment. It is a fact of great moment for species adaptation that the brood normally is sequestered within the stable

environment of the bivouac interior at all times save during the evening emigration, when, as it happens, atmospheric conditions are optimal and very uniform in different localities of the forest. In the susceptible egg stage and at the highly critical stage of hatching, the brood has its most stable environment within the statary bivouac.

Complicating factors arise from both inside and outside the bivouac wall. Sources of atmospheric variation exist not only in an appreciable diurnal range in the extrinsic environment, but also internally, as in the fact that the Eciton brood itself has very different properties of heat radiation according to developmental stage.

However, an appreciable stabilization of microclimatic conditions exists within the bivouac. Control of intra-bivouac temperature through the conservation or release of excessive heat, also a buffering of the brood against external temperature fluctuations is effected to a marked extent through the activities of workers in the bivouac interior and in its wall. The result, although efficient to a very appreciable extent, is not the most precise measure of microclimatic control known for social insects. Some of these insects reach a high standard in this respect. For example, Dunham (1930) found a difference of only 0.7° C between the maximum and minimum temperatures in the brood area of a honeybee hive through a 24-hour period in which extra-hive temperatures varied through a range of 17° C, and various comparable patterns of more or less precise microclimatic control are known for other social insects with permanent nests (Steiner 1926, 1929; Nielsen 1938; Katô 1939; Stahel & Geijskes 1940; Raignier 1948. Obviously, the advantages of a permanent nest pattern with its utilization of physical accessories should not be underestimated for such adjustments. Even so, our evidence suggests that army ants may be relatively high on the list, since atmospheric conditions in the brood area of an Eciton bivouac tend to be stabilized within a limited range intermediate to extremes in the outer environment.

Under a variety of diurnal and seasonal conditions, temperature-control processes within bivouacs of the terrestrial Eciton species normally are such that a regular and stable schedule of brood development is maintained. There is an appreciable variability in the daily march of atmospheric conditions in the Barro Colorado forest (Section 6) as in tropical forests generally (Richards, 1952). During the night, air temperature near the forest floor typically falls to a low around 23° C, but undergoes a rise after dawn to a high around 31° C by noon-time. Thus if brood-area temperature is held near 27° C, as indicated in our records for colony '49 H-34 on the fourth statary day, environmental air temperature would be around 4° C below this level at night and 4° C above it in midday.

The existence of intra-bivouac levelling processes is evident. Some of these enter through the more or less direct responses of workers to outer atmospheric conditions. Such reactions resemble only remotely

some of the behavioral processes of nest-temperature control known for other social insects (e.g., Steiner 1926, 1929; Raignier 1948). For example, the "fanning" of honeybees (Armbruster 1923; Himmer 1932) and of wasps (Steiner 1932) as a reaction to extreme high temperatures of course has no direct counterpart here. As a more comparable process in Eciton colonies, a tighter clustering in the bivouac wall at night operates to conserve intra-bivouac heat under the lower external temperatures which produce the reaction; a stirring about in the daytime results in a more porous bivouac wall and a reduction of bivouac temperature through increased air currents facilitating evaporation. But there is a typical indirectness in daytime behavioral events at the bivouac in relation to microclimatic conditions. For example, the bivouac wall loses ants progressively after dawn as workers join the raiding, excited first of all by the action of light (Schneirla 1940). Once begun, this process is part self-propagated by the excitatory effect of returning traffic, and is also accelerated by general activity through rising external temperatures. Indirectly these changes aid bivouac ventilation both through accounting for an increasing porousness and basal shortening of the outer wall and through a circulation of ants in the interior.

Numerous biological and behavioral factors of evident significance for environmental control underlie the internal organization of a bivouac in the terrestrial Ecitons. As we have shown an Eciton bivouac is organized internally on a gradient basis about the queen and her worker nucleus as well as about the brood. When a larval brood is very young it is concentrated in the very center of the bivouac; at further stages the larger numbers are spread out progressively toward the bivouac margin, the smaller members concentrated near the center (Fig. 1). Thus intra-bivouac conditions are relatively different for the various castes, and increasingly so as development advances. Through the larval stage and later stages of development the brood expands its zone of distribution in the bivouac but maintains its representative gradient pattern. Slight differences in temperature and moisture control dependent upon the size and stimulative properties of brood members may serve as factors in the differential responses of workers to them. We have pointed out some of the adaptive gains of this condition. A further one is conceivable, whereby the larger members of the brood, best able to withstand environmental variations, are stationed at the periphery where their greater ventilation needs in the daytime are assured, with the more susceptible minor castes held to the more stable central areas.

In the evolution of the terrestrial Ecitons, factors underlying the execution of predatory raids evidently arose and became modified in close relation to conditions governing the formation and maintenance of temporary nests. In the contemporary pattern there are numerous indications of this relationship. Examples are found in the development of bivouac-

change processes as a sequel to the daytime raid (Schneirla 1938), and presumably also in the "selection" of optimal nesting sites as an indirect outcome of raiding processes. We have further noted that an acceleration of raiding processes during the morning contributes indirectly to bivouac readjustments which level the internal microclimate against rising environmental temperatures. Finally, when the colony emigrates at the end of a day of raiding, the brood undergoes its only exposure of the day precisely when external conditions are most uniform and are closest to the normal condition of the bivouac microclimate. The rise of factors attuning the daily routine of raiding, emigration and nesting to the diurnal march of environmental events must have played a critical role in the evolution of a terrestrial adjustment in these army ant species.

The New World tropical forest environment in which the terrestrial Eciton have evolved affords habitat conditions with a relatively small range of variation (Richards 1952) as compared with areas outside the forest. Even beyond this the terrestrial Eciton pattern, in its trend away from the ancestral subterranean way of life, has acquired bivouac mechanisms whose dynamic properties further stabilize the microclimate against fluctuations in the general habitat. The rise of the nesting mechanisms must have been basically involved in the emergence of a functional pattern in which highly regular cycles of brood development and colony behavior became closely related systems of events.

It is an important fact that the Eciton pattern requires massive collection activities for all key functions, in raiding and emigrating as well as in nesting. Empirical results and theoretical considerations jointly indicate that a given size colony population is essential to maintain the pattern, and that below this level a colony quickly drops from existence (Schneirla 1949). With sufficient numbers to set up a bivouac which serves as an effective barrier against the raw elements, a colony with a functional queen and hence regular broods can continue to operate normally. In smaller groups, and as individuals, Ecitons lack the ecological resources of insects such as deserticolous forms which can adjust physiologically and often also behaviorally to low atmospheric humidity in particular (Buxton 1923, 1932; Dammerman 1925, 1937; Chapman 1928, 1931; Wigglesworth 1939; Roeder 1952). Subjected experimentally to a degree of atmospheric dryness which for a great many other insects would be termed a moderate condition, Eciton workers soon die. It is probable that normally, exposed when raiding to general environmental conditions which are often hazardous (as at midday) large numbers are lost. The bivouac serves to keep these risks within bounds, in a variety of ways. It is a base of operations in the raid, to which the interchanges of traffic cause most of the workers to return at intervals, probably often enough on the whole to lessen very appreciably the numbers lost through excessive dehydration. Also, in the nomadic phase,

the daily reconstitution of the bivouac in a different locality provides for an alteration of exposure and of recuperation in various sections of the general worker population. Workers forming the basic structure of the bivouac on a given day are last to enter the new structure in the nighttime removal, thus are not hooked fast in place and are available for extra-bivouac function on the following day, when on the other hand raiders of the preceding day may be in a recovery phase as parts of the bivouac structure. In such ways the bivouac may serve as a device for population conservation against the rigors of nomadism and an exposed predatory existence.

The question of population control, complex in any social insect (Bodenheimer 1937; Emerson 1939), seems particularly involved for the Ecitons with their mobile way of life. In most of the population-conservation relations which come first to mind, the bivouac figures prominently. Balanced against inevitable heavy losses through exposure and the hazards of daily combat, new population increments are available regularly in the form of great worker broods. A protected and smooth-running existence for the functional queen within the bivouac assures the presence of successive new broods (Schneirla 1944a); also the bivouac not only provides protection for these broods but an adjusted microclimate as well. Around brood and queen on all sides, and reconstructed daily in the nomadic phase at times of greatest exposure, is a heavy protective wall of workers armed with formidable mandibles and stings. Against voracious potential enemies such as ant eater and coati-mundi, the bivouac offers a bulwark of such effectiveness that these mammals and other possible predators are never observed molesting the army ants. The major worker in particular, with her great, tong-shaped and needle-sharp mandibles, characterizes the terrestrial Eciton species and without question has been an integral factor in their acquisition and maintenance of the terrestrial pattern. Implementing these protective devices as operating also unifies them in its role of population reservoir for the colony.

SUMMARY AND CONCLUSIONS

The temporary nest or bivouac is a key factor in the adaptive pattern of the terrestrial Eciton species studied, essential for their adaptation to a nomadic surface life. This factor in particular admits these species to a life pattern rather different from the subterranean tendency otherwise prevalent in the doryline ants.

The formation of unique temporary nests by the clustering of workers seems attributable to specific organic characteristics such as the recurved tarsal hooks of the workers as well as general characteristics such as the tendency of these ants to assemble in dim light and about their brood and queen.

The establishment of new bivouacs is bound up with the daily occurrence of maximal raids in the

nomadic phase of the activity cycle, when each large foray gives rise to conditions opposing a general return and favoring a continued exodus. Behavioral processes leading to the setting up of new bivouacs are described. In the terrestrial Eciton species of the New World, this resettlement process occurs nightly through each further nomadic phase, during both rainy and dry seasons.

The bivouacs of the terrestrial Eciton species differ strikingly in relation to activity phases. Successive nomadic-phase bivouacs are mainly exposed to the general atmosphere, whereas the cluster maintained throughout each statary phase tends to be enclosed within a natural cavity. This difference is attributed to an indirect process involving behavioral factors such as a greater susceptibility of workers to environmental disturbances (e.g., air currents) when a mature larval brood is present.

Nomadic sites typically approximate the Eciton optimum better than surrounding areas in the general environment and are more stable in their atmospheric properties. A "selection" of sites through a discrimination of atmospheric temperature and humidity by bivouac-founding workers is unlikely; rather, an indirect process is indicated based upon behavior in the transition from raiding to emigration.

Records of the types of bivouac and their locations are summarized and considered in relation to species, activity condition, and seasonal differences. The characteristic cylindrical form of the terrestrial Eciton bivouac, hanging from a natural under-surface to the ground, is considered with its variations in relation to species behavior and to the properties of the terrestrial habitat.

Although the two investigated terrestrial species are broadly similar in the characteristics of their bivouacs, differences also appear. *Eciton hamatum* forms subterranean bivouacs more frequently than does *burchelli*, elevated bivouacs less frequently than *burchelli*. The greater arboreal tendency of *burchelli* is attributed to circumstances arising through the raiding pattern rather than to distinctive responses to an altitudinal atmospheric gradient. The greater frequency of elevated bivouacs in the rainy season and of subterranean bivouacs in the dry season, in both species, also is attributed to differences in the general environmental responses of workers rather than specifically to atmospheric discriminations related to the vertical gradient.

The characteristic tropical forest environment of these Eciton species is described in its general atmospheric properties. Environmental temperature and relative humidity show their greatest daily fluctuation in the dry season. In that season, continuous hygrothermographic records from sites in the general forest environment exhibit a marked day-to-day regularity with an average daily maximum temperature of $28.3 \pm 1.6^\circ \text{C}$ between noon and 3:00 P.M., and an average minimum of $21.9 \pm 1.1^\circ \text{C}$ between 5:00 and 7:00 A.M. Relative humidity readings have an average maximum of $93.4 \pm 1.4\%$ around 9:00 A.M.

and show a sharp drop across midday to a minimum of $71.2 \pm 7.4\%$ around 2:00 P.M. Records from areas such as ridge tops and the windward slope of hills show the greatest diurnal variation.

Local temperature differences on the forest floor are greatest shortly after midday and least between 7:00 and 10:00 P.M.; differences in relative humidity are greatest between 1:00 and 2:00 P.M. and least during the hours around midnight. Significantly, in the nomadic phase transportation of the larval brood in the colony emigration typically occurs in the hours after dusk when temperature and humidity are nearest uniformity throughout the general habitat.

Temperature offered the most feasible means for evaluating temporal changes in the intra-bivouac microclimate. Temperature readings were scheduled at various locations within the bivouac, paired with readings of air temperatures at corresponding vertical levels in the nearby environment. In a series of measurements taken diurnally at regular intervals for each of four different bivouacs of *Eciton hamatum*, internal temperatures almost without exception were higher than outer temperatures by $1-2^\circ\text{C}$ or more. Internal temperatures of both nomadic and statary bivouacs nearly always were found at a level above that of the atmosphere surrounding the bivouac. In both activity phases, intra-bivouac temperatures were less variable from hour to hour than were environmental temperatures.

Through the nomadic phase, intra-bivouac temperatures are higher and vary less than temperatures in the surrounding atmosphere. Stability of internal microclimatic conditions is even greater for statary bivouacs, in which a virtual independence of environmental fluctuations is the rule.

Relative humidity is perhaps the most critical of atmospheric factors affecting terrestrial Ecitons, particularly near the extremes. In controlled laboratory tests Eciton workers engaged in a uniform and continuous activity were found vulnerable to the effects of progressive desiccation. Workers of minor castes succumbed first, the major castes last, with the general lethal point around 50% R.H. (In the natural environment, excessively high temperature and intense light presumably are more or less inseparable from dryness as emergency conditions.) In the dry season especially a prolonged exposure of bivouacs to hazardous desiccation may be not infrequent, as when colonies happen to settle in fallentree areas and on windward slopes. Sustained humidity readings below 60% and near 50% R.H. were found not uncommon in such places. Under such conditions, entire colonies may perish.

Processes have been described which normally permit a routine readjustment of the bivouac microclimate to general diurnal atmospheric variations in the forest at all times of year. Under the influence of occasional localized environmental disturbances (e.g., sun flecks) affecting the bivouac, more or less widespread responses can arise in the population which admit a limited mobility and readjustment. In

the resources of their bivouac, colonies of terrestrial Eciton species have an indispensable aid toward maintaining a regular nomadic cyclic function.

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OAK SEEDLING ECOLOGY DETERMINING SEGREGATION OF SPECIES IN PIEDMONT OAK-HICKORY FORESTS

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INTRODUCTION

The Oak-Hickory Forest Region, as recognized by Braun (1950), extends from Canada to Texas as the westernmost part of the Eastern Deciduous Forest. Oak-hickory communities are also found on the unglaciated lands east of the Mississippi River in the Western Mesophytic Forest Region and in the Oak-Pine Region of the Piedmont and Inner Coastal Plain. Braun suggests that "this [latter] Region might be called the Eastern Oak-Hickory Forest Region."

That the Piedmont belongs to the Oak-Hickory Region has been established beyond doubt by Oosting (1942); the oldest forest stands are oak-hickory and all successional trends lead to final oak-hickory dominance which maintains itself indefinitely if left undisturbed.

The composition of the Piedmont oak-hickory, however, is far from being uniform, qualitatively or quantitatively. Several association-segregates (*sensu* Braun 1935) can be distinguished: the white oak-black oak-red oak, the white oak-post oak, and the post oak-blackjack oak types on the uplands and, in the bottomlands, a type in which more water-tolerant species of oak and hickory predominate. The latter type is considered as postclimax by Oost-

ing (1942) while the post oak-blackjack oak forest is called preclimax or subclimax. From a polyclimax point of view they would be physiographic or edaphic climaxes.

Whatever the terminology used, post oak-blackjack oak forests are restricted, in the North Carolina Piedmont, to dry south-facing bluffs, thin rocky soils, strongly eroded soils, or to the Iredell, Orange and other closely related soil series which are characterized by an extremely impervious and plastic clay a few inches below the surface. From these sites northern red, black, scarlet, and even white oak are almost completely excluded. The trees are slow-growing, rarely exceeding 30 ft. in height, the stands are poorly stocked and do not form a closed canopy.

Similar communities of post oak-blackjack oak exist throughout the Oak-Hickory Forest Region (Braun 1950): (1) in the Flatwoods Belt of Alabama and Mississippi, a flat area of heavy soils, waterlogged during rainy periods, dry and hard at other times; (2) on the poorest soils in the uplands of the Coastal Plain, west of the Mississippi River; (3) on the drier ridges with sandy slopes and steep more or less southerly slopes of the Ozark Plateau, the Boston Mountains, and the Ouachita Mountains; (4) on the open xeric plateau of the western border of the Ozarks; (5) on extensive areas of the old Kansas drift (Mississippi Valley); (6) on the Illinoian drift area (Prairie Peninsula section); (7) in the southern forest-prairie transition, where post

¹ The writer expresses his deep appreciation to Professor H. J. Oosting, who directed this study and the preparation of the manuscript, and to Professors P. J. Kramer and F. X. Schumacher, respectively, for help with the physiological and statistical phases of the work.

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and blackjack oak are the dominant upland tree species and form a savannah climax in some parts of Texas and Oklahoma.

The post oak-blackjack oak community is also represented in the Oak-Chestnut, the Western Mesophytic and the Mixed Mesophytic Forest Region (Braun 1950).

The white oak-black oak-red oak and the white oak-post oak segregates of the oak-hickory association are considered by Oosting (1942) as variants of the oak-hickory climax which are determined by site. The white oak-post oak type is associated with drier ridges and knolls and apparently poorer soils while the white oak-black oak-red oak type occupies the best, mesic upland sites. Quadrat studies showed that the white oak-post oak type differs from the latter by: (1) a smaller (20% less) total basal area, which is a good indication of difference in site quality and stocking; (2) a decreased importance of white oak (19.7% versus 52.1% of the total basal area); (3) an increased importance of post oak (33.9% versus 8.5%); (4) a small increase in southern red oak (5.5% versus 2.9%); (5) the presence of blackjack oak, which is excluded from the other type; (6) a reduced amount of scarlet, black, and northern red oak. Differences are also found in the other elements of the woody vegetation and in the herb layer.

Such synecological studies clarify the details of climax structure and the relationships of successional sequences but raise new questions as to the causes of observed phenomena and practical problems of land management. Such specific questions are likely to be included in one of the following categories: why or how does a given type of vegetation develop in a given environment and not in another; what are, on the one hand, the ecological characteristics of the major species of the community and, on the other hand, the properties of the site which make possible the existence of these species on it?

Studies along these lines have already been made for various successional aspects of Piedmont vegetation: old-field herbaceous and woody succession (Billings 1938; Coile 1940; Kozlowski 1949; Keever 1950; Bormann 1953), bottomland succession (McDermott 1952).

The present paper deals with the climax communities of this region. It is an attempt to explain the segregation of the upland oak species among the three forest types mentioned above: white oak-black oak-red oak, white oak-post oak, and post oak-blackjack oak.

Most of the upland oak species, *Quercus alba* L., *Q. rubra* L., *Q. coccinea* Muenchh., *Q. falcata* Michx., *Q. marilandica* Muenchh., *Q. stellata* Wangenh., *Q. velutina* Lam.,³ were used in some phase of the investigation, which concentrated on germination and seedling stages, the most critical in the life of any plant, even long-lived woody species.

³ Nomenclature from Little, E. L. 1953: Checklist of the native and naturalized trees of the United States (including Alaska). Agriculture Handbook No. 41, Forest Service, U.S.D.A.

Sites on Georgeville and Orange soil series were selected as representatives for, respectively, the white oak-black oak-red oak type and the post oak-blackjack oak type. Both soil series are derived from non-sedimentary parent material, the so-called "Carolina Slate," and belong to the Georgeville soil family (Lee 1947). Although by necessity the work was restricted to the local occurrence of white oak-black oak-red oak and post oak-blackjack oak forest types on particular soil series, it is likely that the conclusions reached, in view of their nature, can be extrapolated to explain the existence of these forest types on other soils and in other regions.

The problem was two-fold: (1) it was necessary to account for the exclusion from poor sites, of the good site (Georgeville) species, such as red oak and also (2) to explain why poor site (Orange) species, such as blackjack oak, are excluded from good sites.

Of the various approaches to the problem, the following were selected as most likely to yield information applicable to its solution:

- (1) survival and growth of seedlings of the various oak species in the field on Orange and Georgeville soils
- (2) responses to drought and the possible causes of differential drought resistance
- (3) sprouting ability
- (4) responses to soil flooding
- (5) effect of light and soil moisture on apparent photosynthesis.

The main body of this paper independently considers methods and results under each of these headings and then, in a discussion, an attempt is made to correlate them in terms of the stated problem.

SURVIVAL AND GROWTH OF OAK SEEDLINGS IN THE FIELD ON ORANGE AND GEORGEVILLE SOILS

The logical first approach to the problem of species segregation by site was to compare survival and growth of representative species from the various forest types, when their acorns were planted together on both good and poor sites. It was hoped that the species would show marked differences that could be correlated with environmental conditions.

OVERWINTER FIELD STORAGE CONDITIONS

Before establishing field plots in the spring, a test was made of the natural overwinter storage conditions offered by Georgeville and Orange soils to acorns of the different oak species.

Acorns of species belonging to the white oak group (subgenus *Leucobalanus*) germinate readily in the fall but do not develop beyond the radicle stage until spring. Acorns of the red oak group (subgenus *Erythrobalanus*), on the contrary, remain dormant and do not germinate before spring. This dormancy was investigated by several workers (Korstian 1927, Brown 1939, MacDermott 1941, Cox 1942) with the final conclusion that it is caused by some inhibiting substance in the embryo (Cox 1942). Seed dormancy can be ruled out as a factor in this problem

since species of both taxonomic groups are represented in each forest type: white oak (subgenus *Leucobalanus*), northern red, black and scarlet oak (subgenus *Erythrobalanus*) in the forest of the good sites, post oak (subgenus *Leucobalanus*) and black-jack oak (subgenus *Erythrobalanus*) on the poor sites.

Dormant and non-dormant acorns overwinter on the ground generally under the litter of the year, since they fall before leaf shedding is completed. During this period, the conditions to which they are exposed are more rigorous on the poor sites than on the good sites. In the poor sites, the soil may be frequently waterlogged during the winter and the scarce litter from the open post oak-blackjack oak stands offers poor protection against extreme fluctuations of temperature and moisture. The acorns of some species may be more sensitive than those of others to these unfavorable conditions and consequently their viability would be strongly reduced on the poor sites.

To test this point, acorns of white, post, blackjack, northern red and scarlet oak, collected locally during the fall of 1952 from seed trees whose identities were certain, were mixed, placed under the litter of a post oak-blackjack oak stand and protected by a wire screen. The same procedure was repeated in a white oak-black oak-red oak stand. These sites were used subsequently for the establishment of field plots I and II. The soil characteristics are described later. The acorns were left in the field until the end of March, 1953, when they were gathered, brought to the greenhouse, planted in pots and checked for successful seedling development. Many acorns were destroyed or removed by animals despite the presence of screens. Only northern red oak acorns, perhaps because of their hard pericarp and bitter taste, were left in sufficient numbers to give truly reliable data. After overwintering on the good site, where this species occurs naturally, 60% of its acorns germinated successfully while the proportion was reduced to 33% after overwintering on the poor site. Comparisons among species could not be made, but the difference observed in northern red oak indicates that reduced seed viability might be one of the causes why some of the species of the white oak-black oak-red oak forest are excluded from the poor sites. This point will be evaluated in the general discussion.

SURVIVAL AND GROWTH IN FIELD PLOTS PROCEDURE

Six field plots were laid out at the end of March, 1953, in the Duke Forest. Plots I, III, and V were located in post oak-blackjack oak stands on Orange soil, plots II, IV, and VI in white oak-black oak-red oak stands, II and IV on Georgeville soil, VI on a transitional zone between Georgeville and Tirzah soils. The Tirzah series is very similar to the Georgeville and differs only by a slightly more clayey surface soil. The plots were so located that an Orange plot would be as near as possible to a Georgeville plot,

the resulting arrangement consisting of 3 pairs of the contrasting conditions.

Soil profile descriptions were made for each location, as well as determinations of field capacity, volume-weight, wilting percentage, mechanical composition and pH of the different horizons. Field capacity of the A horizon was calculated from moisture content determinations of five 100 cc volumetric samples collected with a steel cylinder 36 to 48 hours after a heavy rain. This procedure made it possible to measure volume-weight and to express field-capacity on a volume basis. Bouyoucos's method was used in the mechanical analysis. Wilting percentages were determined with sunflowers. The soil data are presented in Tables 1 and 2.

Each plot, 6 ft. square, was divided into 6 subplots and planted with acorns of the following species: white, post, blackjack, northern red, and scarlet oaks, the species being randomly allocated to the subplots. Two subplots received scarlet oak acorns. The seeds used had been collected the preceding fall from trees that appeared to be relatively free from hybridization, submitted to a floating test for soundness, stratified in moist yellow sand and stored at a temperature of 5° C. Because of the relatively high degree of moisture maintained in the storage containers, most acorns had germinated by the end of March and produced a radicle, rather

TABLE 1. Description of soil profiles in fieldplots.

Plot I	Orange sandy loam
Scant litter	
0 to 2.5cm.	Black sandy loam
2.5 to 20cm.	Yellow-gray sandy loam
20 to 50cm.	Yellow-brown and gray mottled plastic clay loam
50cm. & below	Very friable yellow-brown decaying rock
Plot III	Orange sandy loam
1cm. of litter	
0 to 15cm.	Stony dark brown sandy loam
15 to 30cm.	Yellow-brown sandy loam
30 to 45cm.	Yellow-brown and gray mottled plastic clay
45cm. & below	Friable decaying rock
Plot V	Orange loam
Scant litter	
0 to 2.5cm.	Black loam
2.5 to 10cm.	Yellow-gray friable loam
10 to 45cm.	Red, yellow, brown mottled plastic clay
45cm. & below	Red and yellow decaying rock
Plot II	Georgeville loam
2.5cm. of litter	
0 to 2.5cm.	Black loam
2.5 to 15cm.	Red-brown friable stony loam
15 to 65cm.	Red very friable stony clay
65cm. & below	Red and yellow decaying rock
Plot IV	Georgeville sandy clay loam
5cm. of litter	
0 to 2.5cm.	Dark brown loam
2.5 to 20cm.	Red-brown sandy clay loam
20 to 60cm.	Red very friable clay
60cm. & below	Red and yellow decaying rock
Plot VI	Georgeville-Tirzah loam
5cm. of litter	
0 to 2.5cm.	Dark brown loam
2.5 to 17.5cm.	Dark red-brown loam
17.5 to 75cm.	Red friable clay loam
75cm. & below	Reddish decaying rock

TABLE 2. Soil characteristics of fieldplots.
A=A horizon, B=B horizon.

SOIL SERIES		ORANGE			GEORGEVILLE		
Plot		I	III	V	II	IV	VI
Sand %	A	52.0	56.0	48.0	50.0	45.0	43.2
	B	29.2	19.2	25.2	27.2	19.2	27.2
Silt %	A	34.8	34.8	36.8	30.8	27.8	35.6
	B	33.2	27.2	39.2	27.2	31.2	41.2
Clay % (2 μ)	A	13.2	9.2	15.2	19.2	27.2	21.2
	B	37.6	53.6	35.6	45.6	49.6	31.6
Textural grade	A	Sandy loam	Sandy loam	Loam	Loam	Sandy clay loam	Loam
	B	Clay loam	Clay	Clay loam	Clay	Clay	Clay loam
pH	A 5cm.	4.40	5.40	4.05	4.05	4.75	5.00
	15cm.	4.45	5.70	4.70	4.70	5.15	5.25
	B	4.20	4.70	4.60	4.50	4.90	4.70
Wilting percentage	A	5.18	9.60	5.41	7.96	15.14	8.57
Field ca- pacity %	A	25.81	32.81	22.57	29.07	41.90	34.82
Range of available water %	A	20.63	23.21	17.16	21.11	26.76	26.25

long and often partially suberized except for the tip, in species of the white oak group.

The litter being disturbed as little as possible, 24 holes, narrow but deep enough to accommodate 2 acorns and their radicles were prepared in each subplot. The acorns were carefully planted to avoid breakage of the radicle and covered with litter.

Wire screens were kept over the plots until they started to interfere with the height growth of the seedlings. The screens did not provide complete protection from animals and a number of acorns were destroyed.

Since most acorns germinated before planting and others were destroyed by animals, comparisons among species with regard to germination in the field could not be made. Only seedling establishment and survival could be compared and this was done by expressing the data as percentages of the maximum number of seedlings obtained at any time in each subplot.

Regular inspections of the plots were made throughout the growing season to record survival and observe the appearance of the seedlings. On April 5, June 2, July 13, and August 14, samples were taken from the upper 15 cm of soil for moisture determinations; all these dates but the first followed more or less prolonged dry spells.

On October 1 all surviving seedlings were dug up and brought to the laboratory for determinations of shoot and root length, diameter, oven-dry weight, and measurements of extent of root system.

SURVIVAL

Percentages of survival at the end of the growing season (October 1, 1953) are summarized in Table 3.

TABLE 3. Seedling survival % in fieldplots on
October 1, 1953.

Soil series	Plot	White oak	Post oak	Blackjack oak	Northern red oak	Scarlet oak
Orange	I	64.4	45.5	33.3	37.8	52.0
	III	66.7	54.5	81.1	9.5	34.9
	V	33.3	53.6	100.0	3.3	54.3
	Weighted average	57.6	52.7	75.6	18.8	45.5
Georgeville	II	91.7	50.0	88.9	94.6	89.5
	IV	72.7	93.5	75.0
	VI	31.0	84.0	69.2	64.7	71.1
	Weighted average	66.7	79.3	77.3	84.3	79.2

For the purpose of statistical analysis these data were submitted to the angular transformation: each percentage, $y\%$, was converted to an angle Φ such that $y\% = \sin^2\Phi$. This manipulation resulted in making the variance of each figure independent of its magnitude; consequently the figures could be averaged and the differences between averages tested for significance by means of the t test. The angle values were obtained from the appropriate table in Fisher & Yates (1938). Each was given as weight the total number of seedlings on which the corresponding percentage was based. Weighted averages per soil type were calculated for each species and their weighted sums of square residuals used in testing their differences.

The differences in survival between the Orange and the Georgeville plots were not significant for blackjack oak and white oak. They were, on the contrary, significant at the 2% level for northern red oak, at the 5% level for scarlet oak and the 10% level for post oak.

Survival could also be compared among species in the same soil. There were marked differences in survival between some species on Orange soil. Table 4 gives the averages per species and the level of significance of the differences between any two of these averages. The survival of northern red oak is significantly lower than that of all the other species while blackjack oak has a significantly higher survival than white, scarlet, and northern red oak. On the Georgeville soil, on the other hand, no significant differences in survival were found among the different species.

TABLE 4. Average survival % per species on Orange
soil and levels of significance of their differences.

Weighted average % of survival	Species	White oak	Post oak	Scarlet oak	Northern red oak
75.6.....	Blackjack oak	33.3%	10%	5%
57.6.....	White oak	10%
52.7.....	Post oak	10%
45.5.....	Scarlet oak	10%
18.8.....	Northern red oak

Survival figures do not give a complete picture of the situation. Qualitative observations of the appearance of the seedlings showed marked differ-

ences as well. While post oak and blackjack oak had the same dark green foliage and looked equally healthy on all plots, the seedlings of the other species had on the whole paler leaves on the Orange plots than on the Georgeville ones. Many of the leaves of the seedlings of these species, on the Orange soil, were partially dead or had already fallen by October 1, while on the Georgeville soil, green vigorous foliage was retained until that date (Figure 1).

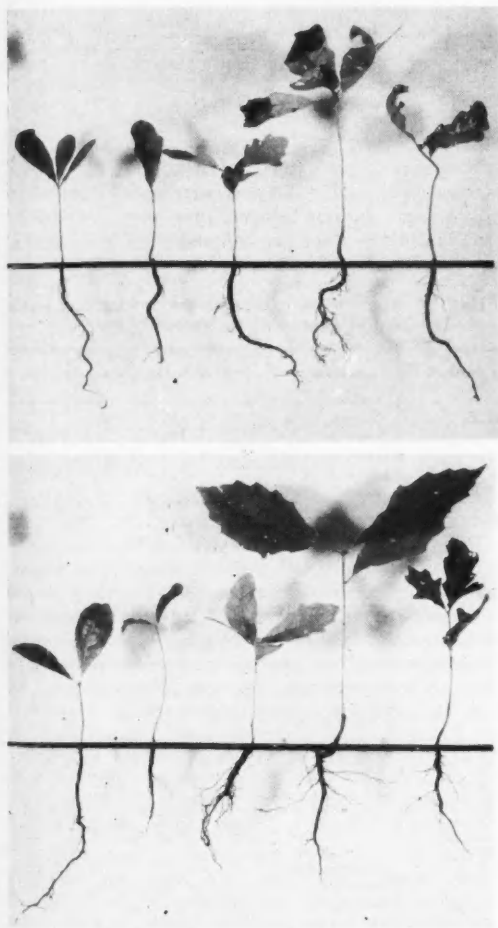


FIG. 1. Oak seedlings grown in Orange (above) and Georgeville soil (below), end of growing season. From left to right: blackjack, post, white, northern red and scarlet oak.

In attempting to correlate these differences in survival with environmental factors, soil moisture was given particular attention since the dying seedlings showed drought injuries. Moreover the summer of 1953 was particularly dry. Data from the Raleigh-Durham airport (U. S. Dept. of Commerce 1953) indicate that only 15.52 in. of precipitation were recorded—9.47 in. less than normal—from April 1 to September 30. The daily and monthly precipita-

tion is presented graphically in Figure 2 which shows that May, July, and August were considerably below normal and that extended periods with negligible precipitation characterized the months of July, August, and September. Soil moisture determinations made at irregular intervals showed consistently and significantly less available water in the upper 15 cm of soil in the Orange plots than in the Georgeville plots (Table 5.) The averages of available water together with the precipitation data and the survival percentages for northern red oak are plotted against time in Figure 2. This graph makes evident the correlation between the survival of northern red oak, the soil type and the amount of available water in the soil during the summer dry spells of this abnormally dry year.

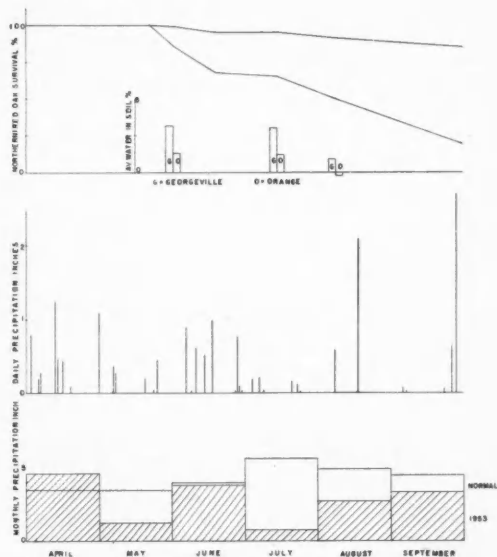


FIG. 2. Survival percentages of northern red oak, available soil water, daily and monthly precipitation. April 1-September 30, 1953. Upper survival curve Georgeville soil, lower Orange soil.

TABLE 5. Available water (actual moisture content minus wilting percentage) in fieldplot soils.

Soil series	Plot	April 5	June 2	July 13	August 4
Orange	I	12.10	1.01	1.15	-.33
	III	14.10	1.81	.56	.31
	V	11.76	.89	1.71	-.34
	Average	12.65	1.24	1.14	-.12
Georgeville	II	15.86	2.41	2.32	.83
	IV	16.84	2.88	3.62	.90
	VI	18.13	4.26	2.98	.73
	Average	16.94	3.18	2.97	.82
Difference between averages significant at the level.....		2%	5%	5%	2%

One environmental factor, which was confounded with soil moisture, and probably affected it to a certain extent, was light intensity. Plots established under the more open canopy of post oak-blackjack oak stands received 40% of full sunlight, on the average, as measured with a standard Weston Illuminometer, those under the white oak-black oak-red oak stands received only about 10%. It is believed, however, that soil moisture was the paramount factor in view of the results of experiments described in later sections.

SEEDLING GROWTH

Total dry weight. The total dry weights of the seedlings were averaged for each species in each plot and the plot averages were then grouped for each soil type. The differences between the weights of the seedlings of a species on the two soil types were not significant but in all species, and particularly in white and northern red oak, the average seedling was somewhat heavier on Orange than on Georgeville soil. This can be explained on the basis of greater selection under the more unfavorable conditions of the Orange site, where only the most vigorous individual seedlings, of northern red, scarlet and white oak especially, survived until the end of the growing season. Furthermore more light reached the seedlings on the Orange plots.

Differences among weights of the seedlings of the various species over all plots were striking. In order of decreasing dry weight the species ranked as follows: northern red, scarlet, white, blackjack, and post oak. The species averages and the levels of significance of their differences are shown in Table 6.

TABLE 6. Average total dry weights per species and levels of significance of their differences.

Average total dry weight gm.	Species	Scarlet oak	White oak	Blackjack oak	Post oak
1.759.....	Northern red oak	1%	1%	1%	1%
1.034.....	Scarlet oak	1%
1.023.....	White oak	1%
.799.....	Blackjack oak	10%
.421.....	Post oak

Shoot-root ratios. It is generally accepted that shoot-root ratios (on an oven-dry weight basis) reflect the environment in which the plants have grown. Thus a relatively low soil water content should result in relatively low shoot-root ratios (Meyer & Anderson 1952).

In this experiment, however, shoot-root ratios did not vary significantly with soil type and consequently with available soil moisture. Differences in shoot-root ratios appeared among species (Table 7) but they agreed with the taxonomic rather than with the ecologic affinities of the species. Those with high ratios belonged to the red oak group (subgenus *Erythrobalanus*), those with lower ratios to the white oak group (subgenus *Leucobalanus*). White oak and post oak, especially the latter, grew a thick taproot,

usually exceeding the shoot in diameter, hence the low shoot-root ratio on a dry weight basis. This condition, therefore, does not necessarily mean that, for the same weight of aerial parts, roots of these species would spread through a greater volume of soil than those of the red oak group.

TABLE 7. Shoot-root ratios per species and levels of significance of their differences.

Average ratio (dry weight basis)	Species	Scarlet oak	Blackjack oak	White oak	Post oak
1.252.....	Northern red oak	10%	10%	1%	1%
.941.....	Scarlet oak	1%	1%
.824.....	Blackjack oak	10%	5%
.494.....	White oak
.443.....	Post oak

Shoot height. The differences in shoot height within the same species between sites were not significant, but there were marked and significant differences among species over all plots (Table 8).

TABLE 8. Average shoot heights per species and levels of significance of their differences.

Average height cm.	Species	White oak	Scarlet oak	Blackjack oak	Post oak
15.05.....	Northern red oak	1%	1%	1%	1%
11.62.....	White oak	...	20%	5%	1%
10.35.....	Scarlet oak	10%	1%
8.50.....	Blackjack oak
7.50.....	Post oak

Shoot basal diameter. The average basal diameters of white oak, post oak, and northern red oak were significantly larger on the Orange plots than on the Georgeville plots. Here again these differences can be attributed to the greater selection of the less favorable habitat. The average diameters per species over all the plots and the levels of significance of their differences are given in Table 9.

TABLE 9. Average shoot basal diameters per species and levels of significance of their differences.

Average shoot diameter mm.	Species	Scarlet oak	White oak	Blackjack oak	Post oak
3.33.....	Northern red oak	5%	1%	1%	1%
2.57.....	Scarlet oak	...	1%	10%	1%
1.95.....	White oak	1%
1.76.....	Blackjack oak
1.32.....	Post oak

Depth of root penetration in the soil. The average depths of root penetration did not vary significantly within nor among species. There was a great amount of variation between individuals of the same species growing on the same plot, especially on the less selective environment of the Georgeville plots.

The maximum depths of penetration observed per plot per species were averaged for each soil type and the differences tested for significance (Table 10). There was a tendency for root systems to grow deeper in Georgeville soil than in Orange soil but the dif-

TABLE 10. Average maximum depths of root penetration per species per soil type and levels of significance of their differences.

Species	AVERAGE MAXIMUM PENETRATION CM.		Difference	Level of significance
	Orange plots	Georgeville plots		
White oak.....	19.0	17.0	-2.0
Post oak.....	13.0	15.0	2.0	1%
Blackjack oak.....	14.7	20.0	5.3
Northern red oak.....	16.7	26.7	10.0	10%
Scarlet oak.....	23.0	25.3	2.5

ferences were rarely significant. The deepest root systems of all species penetrated freely the friable clay of the Georgeville B horizon, which was found from 15 to 20 cm below ground level. In Orange soil the situation was slightly different (Table 11).

TABLE 11. Maximum root penetration per species in Orange soil, cm.

Species	Plot I	Plot III	Plot V
White oak.....	22	17	18
Post oak.....	13	13	13
Blackjack oak.....	11	19	14
Northern red oak.....	23	15	12
Scarlet.....	34	15	20
Depth to B horizon...	20	25	10

Root penetration seems to have been hindered in plot V where plastic clay was found at 10 cm; this was especially true for northern red and blackjack oak. Since both these species seemed to be affected in a similar manner, mechanical resistance of certain soil layers to root penetration can hardly be counted as a factor discriminating against northern red oak in Orange soil. Data on older seedlings would of course be necessary to draw any definite conclusions with respect to this point.

Extent of root systems. To obtain an idea of the three-dimensional extent of root systems through the soil, representative seedlings were laid on paper, their roots arranged in as nearly their natural position in the soil as possible, and their outlines traced on the paper. This procedure, used previously by Ferrell (1949) purposely does not include the whole root system but gives an approximate "cross-section" of it. The areas outlined were measured with a planimeter and the figures obtained were considered as comparable expressions of root extent.

For the same species the average root extent estimated in this manner did not vary significantly between sites. Among species, the root extent of northern red oak seedlings was significantly greater than that of all other species; post oak seedlings had a significantly smaller root extent than all other species (Table 12). These differences in root extent could be expected since northern red and post

oak seedlings ranked respectively first and last in total dry weight, shoot height and diameter.

TABLE 12. Average estimates of root extent per species and levels of significance of their differences.

Average root extent est. (sq. cm.)	Species	Scarlet oak	White oak	Blackjack oak	Post oak
35.1.....	Northern red oak	2%	2%	2%	1%
17.9.....	Scarlet oak	1%
17.4.....	White oak	1%
13.4.....	Blackjack oak	20%
8.5.....	Post oak

In terms of water relations, a plant which would have the greatest root extent per unit of transpiring surface would very likely be best equipped to withstand drought. Such a ratio can be calculated here if the shoot dry weight is accepted as a measure of the amount of transpiring parts and the root extent factor, as determined above, is used as a measure of the extent of root systems. This ratio is probably more meaningful than the root-shoot ratio established on a dry weight basis because of the differences among species in relative importance of the taproot and secondary roots. On these assumptions, the root extent expressed in square centimeters was divided by the shoot dry weight in grams for each seedling. For a species the ratios were generally greater on Georgeville than on Orange soil but the differences were significant only for white oak (at the 5% level). These differences may be a result of the greater resistance to root penetration in Orange soil. In comparing the species among each other over all plots, post oak and white oak had the largest ratios and were significantly different from the other species which, in turn, did not vary significantly among themselves (Table 13). As was true of the shoot-root ratios the grouping of species is more in agreement with their taxonomic than with their ecologic affinities.

TABLE 13. Average root extent—shoot dry weight ratios per species and levels of significance of their differences.

Average ratio	Species	White oak	Blackjack oak	Scarlet oak	Northern red oak
83.20.....	Post oak	20%	20%	10%	5%
56.02.....	White oak	10%	5%
47.06.....	Blackjack oak
41.93.....	Scarlet oak
37.37.....	Northern red oak

SUMMARY OF FIELD PLOT RESULTS

The field data show that acorns of northern red oak tended to be less viable after overwintering in post oak-blackjack oak stands on Orange soil than in white oak-black oak-red oak stands on Georgeville soil. Seedlings of species from the latter forest type, when grown in post oak-blackjack oak stands, survived in considerably lesser proportions than in their natural environment. Seedlings of species from the post oak-blackjack oak forest type survived

equally well in both habitats. There was a strong correlation between the survival of seedlings of species from the white oak-black oak-red oak forest, the soil type and the amount of available water in the soil. Data on growth of the surviving seedlings failed to show any marked difference, for any species, between seedlings grown in one or the other site. The differences among species were consistent: northern red oak made the most growth, followed by scarlet, white, blackjack, and post oak. Even when introduced in the good sites on Georgeville soil the latter two species made poor growth in comparison to northern red oak under the dense canopy of the white oak-black oak-red oak stands.

RESPONSES TO DROUGHT

Field plot data discussed in the preceding section showed a clear correlation between seedling survival of some oak species and amount of readily available water in the soil at critical times of the growing season. Moreover, dying seedlings had all the symptoms of drought-stricken plants. This evidence pointed to differential drought resistance as a possible cause of segregation among oak species. Therefore drought responses of the different species were given particular attention in greenhouse experiments. First an attempt was made to detect the existence of a difference among species in their ability to withstand prolonged soil drought. The result was positive. Then various hypotheses were successively examined to explain such differential drought resistance.

RELATIVE DROUGHT RESISTANCE OF OAK SEEDLINGS PROCEDURE

Acorns kept until the time of planting in moist sand at a temperature of 5° C were potted in a sandy loam characterized by a field capacity of approximately 35% and a wilting percentage of 10.2% on an oven dry weight basis. Five acorns representing each of the following species, white, post, blackjack northern red, and scarlet oak, were planted in each of a set of six-inch clay pots. Another set of pots received 4 acorns: post, blackjack, northern red, and scarlet oak; while a last set was planted with 3 acorns only, one of post, one of northern red, and one of scarlet oak. A layer of vermiculite was spread over the soil to retard evaporation and prevent weed growth. When the seedlings, grown in the greenhouse, had fully developed leaves and a fairly hardened stem, 5 sunflowers were planted in the middle of each pot to serve as indicators of the wilting percentage. The soil was maintained at field capacity until the sunflowers reached a reasonable size (at least 4 leaves). At this time the oaks were two months old. Watering was then discontinued. When the sunflowers showed evidence of permanent wilting, the pots were moved to a shaded part of the greenhouse and left unwatered for various periods of time (2, 3, 5, 7, 11 days) during which temperature and relative humidity were recorded with a hygrothermograph and evaporation was measured

with two white-bulb atmometers. Watering was then resumed and the seedlings were inspected thereafter to check survival and drought injuries. The roots of oaks and sunflowers had spread through the entire relatively small volume of soil of each pot. It was assumed that the soil moisture content was uniformly reduced to the wilting percentage when the drought periods began. At the end of each period, soil moisture content was determined from a random sample of two pots in which two vertical soil cores were taken with a cork borer. An average of 12 seedlings per species were submitted to each drought period except for blackjack oak, for which the average was 8, and white oak which was not represented in the 3 and 5 day periods, because of shortage of adequate plants.

RESULTS

The results are presented in Table 14. Blackjack and post oak clearly surpassed the three other species in withstanding drought. White oak, however, was not found to be superior in this respect either to northern red or to scarlet oak. The possibility of injury from extremely high temperatures or from high temperature-drought interaction can be rejected since the seedlings were kept in the shade where temperatures never exceeded 36° C and reached that level only occasionally for short lengths of time. Conditions were strictly identical for the seedlings of all species: the working unit was the pot in which even-aged seedlings competed for water in the same soil under the same moisture stress.

A sample examination of the root systems of the seedlings considered as dead, that is, those with dead tops, showed that some still had white root tips which reacted positively to the tetrazolium chloride test.⁴ In view of the well-known sprouting ability of oaks, it might be expected that some would survive by producing sprouts. Since there might be specific differences in ability to recover in this way, the "dead" seedlings were kept in soil at field capacity throughout the fall and observed for any evidence of sprouting. During this season a 15-hour photoperiod was maintained in the warm greenhouse. This set of conditions proved successful in preventing dormancy. By December, 22% of the white oak, 62% of the post oak, 18% of the blackjack oak, 30% of the northern red oak and 8% of the scarlet oak seedlings which had had their tops killed by drought had produced sprouts. Considering the relatively small number of plants involved, these differences among species are most likely meaningless, except perhaps where post oak is involved. After the proportion of successful sprouting in each species is accounted for in the evaluation of its resistance to drought, post and blackjack oak retain their superiority over the other oaks.

⁴ This test was made in the same way Parker (1951) used it for coniferous needles. Bits of roots were placed on a deep-well microscope slide previously filled with a 1% 2,3,5 triphenyl tetrazolium chloride aqueous solution and covered with a cover slide to exclude air. After 12 hours in darkness, the material was examined for the appearance of the red color which is supposedly indicative of the presence of active dehydrogenases associated with the living condition.

TABLE 14. Percentages of survival, mortality, and injury in oak seedlings submitted to drought periods.

Days of drought	Min.-max. temp. C.	Min.-max. relative humidity	Evap. cc.	Soil moist. content at end of period	White oak	Post oak	Blackjack oak	Northern red oak	Scarlet oak
2.....	22-36	30-100	...	7.42	100.0	100.0	100.0	100.0	92.3
3.....	20-36	38-100	...	8.91	...	91.7	91.7	91.7	100.0
4.....	20-36	30-100	...	5.95	83.3	85.7	100.0	37.5	77.8
5.....	18-31	35-100	87	6.01	...	75.0	62.5	25.0	25.0
8.....	15-33	38-100	100	5.45	40.0	64.3	42.9	53.3	33.3
11.....	15-33	36-100	136	4.33	0	42.9	16.7	6.7	6.7
Weighted average of survival without injury (2 day treatment excluded).....					43.8	69.1	64.9	43.1	45.8
Weighted average of mortality (i.e. aerial parts dead). (2 day treatment excluded).....					56.2	23.6	29.7	34.5	40.6
Weighted average of injury (2 day treatment excluded)									
Upper leaves dead.....					0	5.5	2.7	6.9	8.5
Upper leaves wrinkled.....					0	1.8	2.7	15.5	5.1

EFFECT OF SOIL DROUGHT AND ATMOSPHERIC DROUGHT ON TRANSPIRATION OF OAK SEEDLINGS

This experiment had several purposes: (1) to compare the transpiration rates of the different species when the soil was maintained at field capacity; (2) to see how different conditions of atmospheric moisture affecting evaporation would affect transpiration; (3) to investigate the effect on transpiration of varying the soil moisture in the range from field capacity to wilting percentage. The effect of soil flooding on transpiration was also studied in the same experiment but is discussed in a later section.

METHODS

During the growing season, one-year-old naturally grown seedlings of white, post, blackjack, northern red, and southern red oak were dug up in the Duke Forest and transplanted to one-quart metal cans previously coated on the inside with an inert antirust compound and on the outside with aluminum paint. The soil used was a sandy loam with a moisture equivalent of 11.6% and a wilting percentage of 4.4%.

To avoid waterlogging, a layer of gravel, one inch thick, was placed in the bottom of the cans. The amount of gravel was so adjusted that the weight of the gravel plus that of the empty can was a constant. To each can 800 gm of air-dry soil (moisture content 1%) was added. Several days were allowed for the seedlings to adjust after transplanting. The cans were then covered with lids made from cut-out bottoms of cans of the same size, diametrically slit to provide passage for the stems of the plants. Electrical tape was used to keep the lids on the cans snugly and to seal the openings around the stems. To allow watering, a small hole was bored through each lid and fitted with a cork stopper. The total combined weight of seedling, lid, tape, and stopper was made constant for each can. This procedure had several advantages: since the system was watertight a weight loss was a direct

measure of transpiration loss; soil moisture content could be readily calculated from total weight; finally, the same total weight corresponded to the same soil moisture content for all cans. Weights were determined to the nearest gram with a Toledo direct-reading scale.

In this experiment, six species (the sixth was turkey oak, *Q. laevis* Walt., not discussed here) were submitted to 3 soil moisture treatments: field capacity, drought (above wilting percentage) and flooding. Each species-treatment combination was replicated 6 times, making a total of 108 phytometer cans arranged in a completely randomized design. A number of seedlings died during the experiment, thus reducing the number of replications in some species. To prevent overheating of the soil, the cans, which were exposed to full sunlight in the greenhouse, were placed in metal tanks filled with water. During the warmest days water was changed several times a day so that the soil temperature never exceeded 35° C. Temperature and relative humidity were recorded with a hygrothermograph and evaporation was measured with two white-bulb atmometers.

Leaf areas were measured by placing the leaf, attached to the seedling, under a transparent plastic sheet. The tracer point of a planimeter could thus be slid over the plastic sheet without being in contact with the leaf.

There were 18 seedlings of each species to assign to 3 treatments. All other conditions being equal, transpiration rates generally vary widely among individuals. The following procedure was used to insure an approximately equal range of variability among the seedlings comprising the 6 replications of each treatment. The soil being maintained at field capacity, the transpiration rates of the seedlings were measured daily for a period of 8 days. On the basis of these rates, expressed per unit of leaf area, the 18 representatives of each species were distributed among three groups: those with high, medium,

and low rates. Two seedlings from each of these groups were then randomly selected to be assigned to each treatment. Consequently, each treatment was applied to 6 plants including 2 with high, 2 with medium, and 2 with low rates.

In the cans assigned to the first treatment, field capacity was restored after each weighing by adding the amount of water equivalent to that lost through transpiration. In the second treatment the soil moisture was allowed to decrease from the moisture equivalent down to the wilting percentage. Transpiration loss and amount of soil moisture were calculated from the daily weighings. At each weighing the cork stopper was removed to permit ventilation of the cans. In the third treatment the soil was flooded, the water level being maintained just above the soil surface.

Transpiration rates at field capacity were expressed in mg of water per sq cm of leaf area.

For the two latter treatments, the rates for any day were expressed in percent of the expected rate for that day, had the seedlings been in a soil at field capacity. To arrive at these figures the following computations were made:

1. the rates for the control plants (those at field capacity) were averaged for each day.
2. the daily rate for each treated plant was divided by the average rate for the controls on that day; for the flooded seedlings, the average rate of all replications could be directly divided by the average control rate, since there were no variations in soil moisture among the replications.
3. the rates for the controls, prior to the start of treatments when all soils were maintained at field capacity, were divided by the rates, for the same period of time, of the seedlings that were to be assigned to each of the treatments.
4. this fraction was multiplied by the fraction obtained in 2.

The resulting figure is the best possible estimate of the transpiration rate of a seedling submitted to drought or to flooding in percent of the rate it would have if the soil were at field capacity.

RESULTS

Transpiration Rates with the Soil at Field Capacity

Over a 48-day period, during which 37 series of measurements were made, the seedlings in a soil at field capacity had the following average daily transpiration rates in mg of water per sq cm of leaf area:

white oak	55.5
post oak	100.5
blackjack oak	107.6
northern red oak	65.5
southern red oak	83.0

During the same period of time the average atmometer loss was 19.02 cc of water per day. In spite of their magnitude the differences among average rates were not statistically significant because

of great variability in individual measurements. These data show that post and blackjack oak are by no means more thrifty in their water economy than the other species, at least when soil moisture is plentiful. On the contrary, although the differences were not significant, their rates tended to be higher, despite the thickness and the leathery character of their leaves.

Effect of Atmospheric Conditions on Transpiration Rate

Atmometer data are an integrated expression of atmospheric drought. For the same soil moisture content, say field capacity, transpiration rates will vary with the amount of evaporation as measured with atmometer bulbs. To see if the species would show a differential transpiration response to various atmospheric conditions, the data from three days with distinct rates of evaporation were examined. These days were characterized by, respectively, a low (11.9 cc), a medium (21.9 cc), and a high (29.6 cc) atmometric evaporation. The transpiration rates, in mg of water per sq cm of leaf area, averaged for all the replications of each species-evaporation rate combination, and the analysis of variance of the data are given in Table 15. Atmospheric conditions proved to have a significant effect on transpiration rate but there were no significant differences among species for all evaporation rates nor was the interaction between species and atmospheric conditions significant. In other words, the transpiration rates of all species were affected in the same manner by atmospheric conditions resulting in high, medium, and low evaporation rates.

TABLE 15. Average transpiration rates in mg per sq cm of leaf area under different evaporation rates in cc of water and analysis of variance.

Species	EVAPORATION RATE		
	Low 11.9 cc.	Medium 21.9 cc.	High 29.6 cc.
White oak	70.3	97.0	80.0
Post oak	55.0	151.3	169.0
Blackjack oak	79.0	162.3	174.7
Northern red oak	36.0	91.3	94.3
Southern red oak	53.0	144.0	112.0

Source of variation	Sums of squares	Degrees of freedom	Mean square	F ratio
Species	2318.6	4	579.65	.2579 Not sign.
Evaporation rate	43157.4	2	21578.70	9.5766 Sign. 1%
Interaction sp.-evap.	34421.6	8	4302.70	1.9095 Not sign.
Error	67598.3	30	2253.28	
Total	113074.3	44		

Effect of Reduced Moisture Content on Transpiration Rates

Transpiration rates of each seedling in this treatment were measured at intervals as the soil water content declined and until soil moisture in each can was reduced at least to the wilting percentage. The rates, expressed in percent of the expected rate at

field capacity as described previously, were plotted against soil moisture content (Figure 3). Each point represents the average rate of all seedlings of a species for the same soil moisture content. Since soil moisture did not decrease uniformly in all cans of the same species due to individual variability and differences in seedling size, each average was calculated from rates that were not necessarily measured on the same day. This procedure could be followed because each individual reading was divided by the rate of the controls for the same time-interval.

The graphic comparison fails to show any striking difference in behavior among the species and statistically significant differences were not found. The rates of transpiration of post and blackjack oak are least and most reduced, respectively, as soil moisture decreases down to the wilting percentage, while northern red, southern red, and white oak occupy intermediate positions. The evidence suggests that, in all likelihood, differences in the reduction of transpiration rates at low soil moisture levels are insufficient to account for differential drought resistance among oak species.

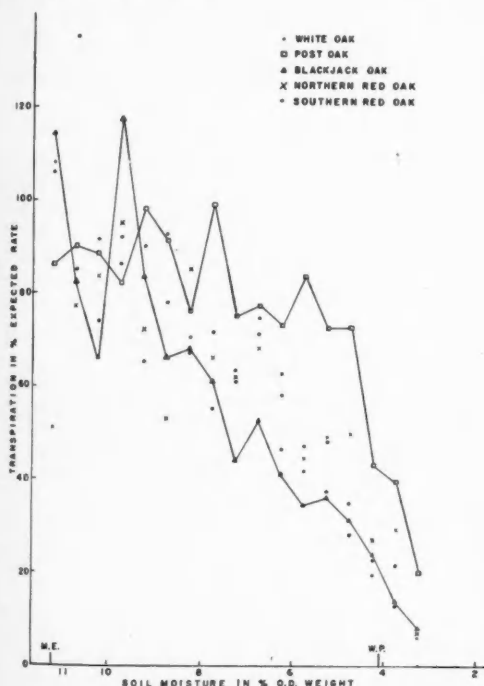


Fig. 3. The effect of decreasing soil moisture on transpiration of oak seedlings. The general trend is illustrated by the curves drawn for post and blackjack oak.

LEAF MOISTURE CONTENT IN RELATION TO SOIL MOISTURE CONTENT

That leaf moisture retention at low soil moisture levels is related to drought resistance has been proposed by some authors. Parker (1951), for instance,

found that needles of ponderosa pine, which is more drought resistant than Douglas fir and western arbutus, retained more moisture than those of the latter two species when exposed to desiccation.

Another view on drought resistance, held by Maximov (1929) and others, is that tissues of drought resistant plants can withstand a greater degree of dehydration without losing the ability to recover turgidity when the water supply is restored.

The following experiment was designed to investigate characteristics of oak species with regard to these two points.

METHOD

Eight species represented by 2½-month-old seedlings, grown individually in 4-inch clay pots, were included in this test: white, post, blackjack, northern red, southern red, scarlet, black, and chestnut oak. Out of four pots for each species, two were maintained at field capacity, while watering was discontinued for the other two. When the decreasing soil moisture content reached the wilting percentage, as indicated by sunflowers grown with the oaks, the relative humidity in the greenhouse was raised to saturation during the night by repeated watering of walks and walls so that constant conditions of humidity (and temperature) would prevail during leaf sampling. Two leaves of each seedling in each treatment were then cut and immediately weighed to the nearest 5 mg. The samples were transferred to individual moisture chambers made of pint, watertight, cardboard containers holding a layer of water 1 cm deep. The leaves were placed in an upright position with the base of the petiole under water. The extremity of the petiole was then cut off under water to reduce plugging of the vessels. The leaves in their chambers were subsequently placed together in a container where 100% relative humidity was maintained. The entire unit was kept in a constant temperature room (25° C). When the leaves reached a constant weight, as evidenced by sample weighing, they were assumed to be saturated with water and the corresponding weights were determined. They were subsequently oven-dried at 105° C and reweighed. Leaf moisture content at the time of sampling was then calculated in percent of oven-dry weight and the leaf water saturation deficit was expressed by the formula used by Stocker (1929), Killian (1947), and Arvidsson (1951):

water saturation deficit = $\frac{\text{water content at saturation} - \text{actual water content}}{\text{water content at saturation}}$; or deficit % = $\frac{\text{saturation weight} - \text{actual weight}}{\text{saturation weight} - \text{oven dry weight}}$

A slight error is introduced by the loss of dry matter through respiration during the stay in the moisture chamber but such a loss is negligible when compared to the total dry weight.

RESULTS

Leaf Moisture Contents with the Soil at Field Capacity

The leaf moisture contents when the soil was at field capacity, expressed in percent of oven-dry weight, varied little among species and the small differences were not statistically significant (Table 16).

TABLE 16. Average leaf moisture contents in % of oven-dry weight. Soil at field capacity.

White oak.....	262.5	Scarlet oak.....	237.8
Post oak.....	262.0	Black oak.....	250.8
Blackjack oak.....	262.0	Southern red oak.....	256.5
Northern red oak.....	252.0	Chestnut oak.....	282.8

Water Saturation Deficits of Leaves with the Soil at the Wilting Percentage

Highly significant differences were found between the average deficits of some species. The ranking of the species (Table 17) in the order of increasing water saturation deficit at low soil moisture content corresponds exactly to the ranking in the order of decreasing mesophytism as judged from field observations, or of increasing drought resistance as previously discussed. The deficits of blackjack, post, and to a certain extent southern red oak, were markedly and significantly higher than those of all other species. The deficits for chestnut, white, northern red, scarlet, and black oak were not significantly different.

These differences are such that the hypothesis of leaf moisture retention associated with drought resistance cannot apply to oak species. Contrary to this hypothesis, the most drought resistant oak species were those which retained least moisture in their leaves. The fact is that the latter species had their leaf water content reduced appreciably lower than that of the less drought resistant ones and yet all individuals fully recovered turgidity when watering was resumed. This seems to indicate that drought resistant oaks can withstand successfully a greater degree of leaf desiccation than non-resistant ones, a character most likely related to the physico-chemical properties of their protoplasm.

OSMOTIC PRESSURE OF THE CELL SAP

Osmotic pressure has often been correlated to drought resistance. Höfler *et al.* (1941) found that

drought resistant species in general have a high osmotic pressure, but there are numerous exceptions. The different oak species were tested to see if they would vary considerably in this respect.

Seedlings grown in the greenhouse under strictly identical conditions, in a soil kept at field capacity, were used for the determinations. The leaves were removed at the same time and stored in waterproof bags at a temperature below freezing. After thawing, the cell sap was extracted by applying a uniform pressure of 320 kgs/sq cm. The undercooling and freezing-point depression of the sap were determined with a regular cryoscopic thermometer. Using the undercooling factor (Harris *et al.* 1925) and the freezing-point depression, osmotic pressures were calculated as follows:

White oak	8.3 atmospheres
blackjack oak	9.8 "
northern red oak	10.8 "
scarlet oak	8.4 "

Such small differences could hardly be meaningful.

Bound water determinations were made by Kramer, Pawek, and Korstian (Korstian 1933) for several Piedmont tree species including red, post, and blackjack oak. The values found were, in the order, 46.41, 41.91, and 56.52, showing no correlation with the degree of drought resistance.

CONCLUSIONS

Arvidsson (1951), reviewing the work of Maximov (1929), Walter (1931), and Stocker (1929, 1942, 1948), proposed the following concepts of drought resistance: drought resistance, in the broad sense, is the ability of a plant to grow in dry habitats and survive dry periods. There are two main types: active and passive drought resistance.

Passive resistance is the ability of a plant to withstand drought by entering a resting stage.

Active resistance does not involve any such stage. It can be primary or secondary. Primary drought resistance is the ability of the plant tissues to withstand dehydration. It is the same as Iljin's concept of desiccation resistance (1927). It is related to the physico-chemical properties of the protoplasm. Several theories of drought resistance have been proposed and are reviewed by Levitt (1951); they are often diametrically opposed and none is really satisfactory.

Secondary drought resistance is the ability of

TABLE 17. Leaf water saturation deficits % and levels of significance of their differences.

Saturation deficit %	Species	White oak	Northern red oak	Scarlet oak	Black oak	Southern red oak	Post oak	Blackjack oak
1.65.....	Chestnut oak	1%	1%	1%
2.16.....	White oak	1%	1%	1%
4.84.....	Northern red oak	5%	1%	1%
5.23.....	Scarlet oak	5%	1%	1%
9.50.....	Black oak	5%	1%
15.66.....	Southern red oak	10%
20.60.....	Post oak
25.04.....	Blackjack oak

the plant to prevent dehydration. Such an ability could result from a relatively great root extent and/or from a reduction in transpiration losses during periods of moisture stress.

The oak species studied here show neither of these properties. The shoot-root ratios of northern red and blackjack oak, to take two extreme examples of drought resistance, are not very different and, in general, the shoot-root ratios are more related to taxonomic rather than to ecologic affinities. Nor do the roots of blackjack oak reach greater depths in the soil than those of northern red oak. Furthermore, the factor of root extent could be ruled out in the experiment which established the existence of a differential drought resistance among oak species since the seedlings were grown together in a small volume of soil. On the other hand, transpiration losses with soil moisture near the wilting percentage were not reduced to a greater extent in drought resistant than in non-drought-resistant oaks. Neither did osmotic pressure nor bound water determinations show any difference in these respects among species. By the process of elimination it must be concluded that the drought resistance of post and blackjack oak is of the primary kind. This is confirmed by the fact that greater water saturation deficits exist in seedlings of these species when the soil is at or below the wilting percentage. Yet, they will recover, when soil moisture is increased, with greater success than seedlings of the non-drought-resistant species. More work should be done, of course, to clarify this question. Tentatively it is suggested that the cause of greater drought resistance in some oak species lies in their ability to withstand a greater degree of desiccation of their tissues and still recover turgidity when the water supply is restored.

SPROUTING ABILITY

Oaks have the ability to sprout vigorously when the shoot has been cut or killed back. Numerous buds are formed on one-year-old stems but they do not develop into branches immediately. These are not dormant buds, strictly speaking, since, although they do not unfold, each year the bases of the stem tips increase in length an amount equal to the width of the annual ring, thus keeping the bud on the outside of the wood. The bud traces so formed are dwarfed, greatly modified branches, encased in the xylem of the main stem. The sprouts which develop from these buds are in reality branches whose development has been delayed (Liming 1940). Oak buds are thus essentially different from the adventitious buds formed in other trees (beech, for example) as a direct consequence of shoot removal. Whenever an abundant supply of water and solutes is available to them, the "dormant" oak buds develop into vigorous sprouts. As a matter of fact, some old silvicultural practices (coppice system) are based almost entirely on this property.

When an oak seedling has its shoot killed or seriously injured by drought or any other cause, it may still survive by subsequent sprouting. There-

fore, it seemed desirable to see if any difference could be detected in the sprouting ability of the various species.

For each species, three groups of seedlings, grown in the greenhouse and 3, 4, and 5 months old, respectively, were submitted to a sprouting test. The shoots were cut just above the level of insertion of the cotyledons and subsequent sprouting was recorded. At all times, the soil was maintained at field capacity. The weighted average percentages of sprouting after two months, over all age-groups, were: 36.6 for white oak, 49.2 for post, 52.6 for blackjack, 45.8 for northern red, 22.2 for scarlet, and 50.0 for southern red oak. The differences between these averages were not statistically significant.

More data on sprouting ability were obtained from the seedlings used in the drought resistance experiment and were presented in the preceding section. They failed, as well, to show any difference between species with respect to sprouting ability.

RESPONSES TO SOIL FLOODING

The Orange, Iredell, and other soil series supporting post oak-blackjack oak forests are characterized by an impervious clay or clay loam B horizon. Consequently, on level surfaces, such soils can be waterlogged at times, especially during particularly rainy seasons. The possible role of this factor in segregation of species by site was investigated by submitting seedlings to soil flooding in controlled conditions, and observing the resulting effect on survival and transpiration.

EFFECT OF SOIL FLOODING ON TRANSPIRATION METHOD

Six seedlings each of white, post, blackjack, northern red and southern red oak, in tight metal cans, were exposed to soil flooding for a 55-day period. This treatment was a part of the general transpiration study already discussed. The experimental procedure and the method of calculation of data were described earlier (p. 306) and thus need not be repeated here.

RESULTS

Transpiration rates under flooding conditions, expressed in percent of expected rates at field capacity are presented graphically in Figure 4. Each plotted point represents the average of all replications of the same species. These averages are affected by standard errors of such magnitude that differences among species are not significant. For all species, except northern red oak, transpiration rates increased immediately after flooding was initiated to reach a peak above 100% of the expected rate within the next 24 to 48 hours. Then rates declined, rapidly at first then more and more slowly as time went on. After about 30 days of continuous flooding they remained stationary until the end of the experiment at values ranging from 22% (blackjack oak) to 56% (post oak) of the expected rate at field capacity.

Similar trends have been reported by Parker (1950) for loblolly pine, red cedar, overcup and

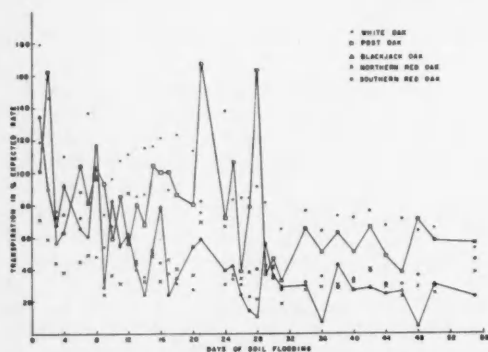


FIG. 4. The effect of soil flooding on transpiration of oak seedlings. The general trend is illustrated by the curves drawn for post and blackjack oak.

swamp chestnut oak and by Kramer (1951) for tomato and privet. The initial increase in transpiration corresponds to an increase in water absorption which occurs, according to Kramer, because cells are killed by a high concentration of CO_2 and resistance to water movement across the cortex is decreased. The subsequent decline in water absorption would be due chiefly to plugging of the conducting system partly by bacterial activity, partly by accumulation of gum. The stabilization of transpiration rates after 30 days in the present experiment is probably a result of the water absorbing activities of the newly formed adventitious roots described below. The fact that northern red oak seedlings did not exhibit the initial rise in transpiration may indicate that the increase in permeability was followed more rapidly than in the other species by plugging of the vessels, the whole process occurring within the first 24 hours after flooding, before the first measurements were taken.

EFFECT OF SOIL FLOODING ON SURVIVAL

When the seedlings used in the preceding experiment were uprooted after 55 days of continuous flooding most of them were still living. As a matter of fact, several white, northern red, and post oaks had grown new leaves during this period. Some of the original leaves had died and abscised, while others showed injuries at the tips and/or margins.

Almost all seedlings in all species had developed thin, highly ramified adventitious roots extending radially in all directions in a horizontal plane just above the surface of the soil but under the water level. Some of these roots reached over 10 cm in length. Most of the pre-existing roots were brown and rotten but some still showed white tips.

In all species many seedlings were found to be slightly buttressed at the collar. They showed in the same region (about 1 cm above soil surface to 3 cm below) snow-white, knoblike, apparently parenchymatous proliferations. These arose from the lenticels and the small longitudinal cracks of the bark, and often they would surround the insertion point of an adventitious root. They were best developed

on northern red oak seedlings, where some protruded as much as 2 mm from the stem. Similar structures were observed by Kramer (1951) on tulip poplar.

A second flooding experiment was conducted during the summer of 1953. Four-month-old seedlings grown in clay pots were randomly located in a metal tank and flooded for 64 days, the water level being maintained just above the surface of the soil. At the end of this period, the percentages of survival without apparent injury were as follows: 57.1 for white oak, 77.8 for post oak, 36.8 for blackjack oak, 34.8 for northern red oak, and 30.4 for scarlet oak. Injuries consisted of pale, wrinkled, wilted, or dead leaves. Some leaves also were covered with aphid secretions. The white proliferations and buttressing mentioned previously were found here as well. The survival figures indicate that blackjack oak was as much affected as northern red oak by prolonged flooding. The relatively higher percentage of survival of post oak seedlings is of little significance because it is based on a considerably smaller number of plants than the corresponding percentages for the other species.

The results of these experiments suggest that resistance to flooding may not be a factor in the segregation of species by site. The seedlings of all the upland species considered here successfully withstood flooding for relatively short periods of time but of a length comparable to those they might encounter in the field during the growing season. Injuries and mortality appeared only after long periods of soil waterlogging, and then species as far apart ecologically as northern red and blackjack oak were similarly affected.

EFFECT OF LIGHT INTENSITY AND SOIL MOISTURE ON PHOTOSYNTHESIS OF OAK SEEDLINGS

The effect on plant growth of environmental factors such as light intensity or soil moisture can be assessed in two ways. The first involves evaluating the cumulative effect of the factor under consideration in terms of the increment of dry matter over an extended period of time, say one or more growing seasons. The second is to measure the effect of the factor studied on the net assimilation rate at a given moment of the life of the plant. Both methods were used but destruction of plant material during the course of the growth experiment made it worthless. This section is thus concerned only with measurements of assimilation rate.

GENERAL METHODS

Rates of apparent photosynthesis were measured in terms of CO_2 uptake per unit of time per unit of leaf area. The apparatus used was that described by Decker (1944) and Kozłowski (1949) but the procedure had to be modified. These authors used an open system and measured CO_2 uptake of plants placed inside chambers under controlled conditions by comparing the CO_2 concentration of the air before and after its passage through the chamber. In the

present study, the size of the plants, and consequently their photosynthetic rates, were too small to reduce the CO_2 concentration of flowing air in amounts sufficient to permit accurate measurements. It was decided, therefore, to use a closed system and to calculate photosynthetic rates from the rate of decrease of the concentration of CO_2 inside the system. Concentrations of CO_2 were measured, as Kozlowski (1949) had done previously, with a Grubb-Parson Infrared Gas Analyzer.

The details of construction of the closed system were as follows. A lucite plate, 17.5 cm in diameter, 5 mm thick and radially slit to fit around the seedling stem, was laid on the top of the clay pot containing the plant. An I-shaped lucite slide joined the edges of the slit. Its extremity almost reached the center of the circular plate. Permagum, an inert sealing compound, was used to stop the openings left in the center around the seedling stem. A glass cylinder, 30 cm long and 14.5 cm in diameter, was then inverted over the lucite plate so as to enclose the aerial parts of the plant without interfering with their natural position. The ground glass edge of the cylinder, as well as the margins of the slide, were sealed to the plate with a high vacuum inert silicone compound. Two holes had been previously bored through the base to provide passage for inlet and outlet tubes. The outlet tube was connected to an aquarium type diaphragm pump (rate of flow 3 l/min.) which sent the air through a silica gel dehydrating tube to the gas analyzer. A manometer was mounted in parallel on the line before it reached the gas analyzer. The air was circulated back to the chamber from the analyzer through the inlet tubing.

The potted seedling, surmounted by the glass chamber, was placed inside the refrigerated cabinet of the original Decker (1944) apparatus and illuminated by a battery of enclosed-reflector Mazda lamps. A blanket of running water, about 2.5 cm deep, was maintained on the top of the glass cabinet to absorb the heat of the overhead lamps before it reached the chamber.

At the beginning of each run, enough CO_2 was injected into the system to increase the concentration to a level about 15% above that of normal air. As photosynthesis proceeded, the CO_2 concentration of the system dropped. The time-interval required for a decrease in concentration from 10% above to 10% below normal air concentration (0.03%) was measured. Since such a time-interval is inversely proportional to the rate of CO_2 uptake by the plant leaves, rates of apparent photosynthesis could be calculated easily, knowing the internal volume of the system. The $\pm 10\%$ range around normal CO_2 concentration was selected on the basis of Decker's (1944) finding, that photosynthesis was not retarded when less than 15% of the atmospheric content of CO_2 was removed.

The oaks tested were 2½-month-old seedlings, grown in individual 4-inch clay pots, inside the greenhouse, using the same soil as in the drought

resistance experiment described previously. Prior to testing, they were protected from extremes of temperature and light intensity to avoid differential preconditioning that might differently affect subsequent rates of photosynthesis. Before each determination, they were given at least 15 minutes to get adjusted to the new conditions existing in the chamber. Such a length of time had been found sufficient by Kramer & Decker (1944).

The experiments were performed to compare the growth requirements of northern red and blackjack oak. These two species were selected because they represent two extremes of the series of oaks species if arranged in the order of decreasing mesophytism, and increasing drought resistance.

In the first experiment photosynthetic rates were measured under different light intensities, the soil being maintained at field capacity. The second experiment, on the other hand, tested the effect of soil moisture on photosynthetic rate, in the range from field capacity to wilting percentage, under a constant light intensity.

EFFECT OF LIGHT INTENSITY OF THE APPARENT PHOTOSYNTHESIS OF NORTHERN RED AND BLACKJACK OAK

METHOD

Apparent photosynthetic rates were measured under six different light intensities: 400, 690, 1000, 1800, 4000, and 8500 f.c. These light intensities were obtained by using various combinations of lamp numbers and cheesecloth screens. They were estimated from the average reading of a Weston Illuminometer placed at the location of the seedling leaves under the glass chamber. The light intensity levels selected were in an approximate geometric progression rather than in arithmetic progression since it is known that photosynthetic rates plotted against light intensity generally form a hyperbolic curve.

Six seedlings of each species were included in the test. The rates of each seedling under each of the light intensities were measured in succession, starting with the lowest level. To compensate for a possible effect of time of day on photosynthetic rate, half of the seedlings of each species were run in the morning, the other half during the afternoon.

Temperature was difficult to control under varying light intensity since the inside of the chamber was not refrigerated. Nevertheless, by regulating refrigeration around the chamber and the flow of water on top of the cabinet, temperature could be kept between 25 and 31° C from one day to the other and it varied much less during the time each individual plant was run. Since rates were expressed as percent of maximum observed for each seedling, before being analyzed statistically, the variation due to temperature differences was reduced to a minimum.

RESULTS

The average rates for each species at each light intensity are expressed in Table 18 in three different

manners: per seedling, per sq cm of leaf area, and in percent of observed maximum.

TABLE 18. Average apparent photosynthetic rates of northern red and blackjack oak as a function of light intensity.

Light intensity (f.c.)	Rate per seedling mg. CO ₂ /minute		Rate per sq. cm. leaf area mg. CO ₂ /minute		Rate in % of observed maximum	
	Northern red oak	Blackjack oak	Northern red oak	Blackjack oak	Northern red oak	Blackjack oak
400.....	.08773	.05017	.00047356	.00055147	35.9	23.1
690.....	.17511	.09520	.00096883	.00103258	73.5	43.2
1000.....	.19729	.12938	.00100079	.00140974	82.8	59.0
1800.....	.25070	.17870	.00128399	.00195649	97.4	81.0
4000.....	.23193	.21166	.00131774	.00226895	100.0	95.0
8500.....	.18397	.22021	.00101300	.00289943	76.9	100.0

In the analysis of variance (Table 19) the experiment was considered as having a split-plot design with light the major factor and species the minor factor. Rates in percent of observed maximum were used in the computations. Since these values varied less between species than either of the other expressions of the results, any significant difference among them will be all the more significant when expressed per unit leaf area or per seedling.

TABLE 19. Analysis of variance of photosynthetic rates of blackjack and northern red oak at different light intensities expressed in % of observed maximum.

Source of variation	Sums of squares	Degrees of freedom	Mean square	F ratio
Light.....	34650.7181	5	6930.1436	65.0740 Highly sign. (0.1%)
Replications.....	1135.1665	5	227.0333	2.1318 Not sign.
Error.....	2662.3994	25	106.4960	
	38448.2840	35		
Species.....	2290.5170	1	2290.5170	32.7513 Highly sign. (0.1%)
Interaction light-species.....	4949.6222	5	989.9244	14.1572 Highly sign. (0.1%)
Error.....	2097.7158	30	69.9238	
Total.....	47786.1390	71		

The analysis of variance indicates that light intensity, species, and light-species interaction all had a highly significant effect on photosynthetic rate.

For all light intensities except 8500 f.c., the rates in % of maximum for northern red oak were higher than those of blackjack oak. At 8500, the reverse was true. The differences between species and their degree of significance are shown in Table 20.

Variations of photosynthetic rate with light intensity were markedly different in the two species (Table 18). Rates of blackjack oak seedlings increased continuously and significantly with increasing light intensity while in northern red oak seedlings, the initial increase was strong but the maximum rate was almost reached at 1800 f.c. The decrease in rate of northern red oak seedlings above 4000 f.c. may be due not only to the effect of light but also to the effect of the higher temperatures prevailing

TABLE 20. Levels of significance of the differences a) between photosynthetic rates for the same species at different light intensities; b) between rates for the two species at the same light intensity.

a) same species at different light intensities

Light intensity (f.c.)	BLACKJACK OAK		NORTHERN RED OAK	
	Rate in % of max.	Difference significant at	Rate in % of max.	Difference significant at
400.....	23.1		35.9	
690.....	43.2	1%	73.5	1%
1000.....	59.0	1%	82.8	10%
1800.....	81.0	1%	97.4	5%
4000.....	95.0	5%	100.0	...
8500.....	100.0	40.%	76.9	1%

b) between species at same light intensity

Light intensity (f.c.)	Rates in % of maximum (northern red-blackjack oak)	Level of significance
400.....	12.9	5%
690.....	30.0	1%
1000.....	25.3	1%
1800.....	16.0	1%
4000.....	4.9	33%
8500.....	-20.9	1%

in the chamber under the high light intensities, or to the interaction of these two factors. Whatever the real cause, blackjack oak seedlings were exposed to identical conditions and their response was quite different.

The effect of time of day on photosynthesis was found to be of no significance.

The results of this experiment demonstrate the shade tolerance of northern red oak seedlings and the intolerance of blackjack oak seedlings. Under low light intensity and in a soil at field capacity, northern red oak seedlings are able to carry on photosynthesis, and thus accumulate dry matter, at a higher rate than blackjack oak seedlings. They reach their peak of photosynthesis at a relatively low light intensity. Their rate decreases under strong light and with the high temperatures usually associated with it, in the field even more than in this experiment. Under the same conditions the photosynthetic rate of blackjack oak seedlings still increases. These differences between species are best shown when absolute rates per seedling are graphed, instead of relative rates (Fig. 5). At a point between 4000 and 8500 f.c., the rates of seedlings of both species became equal.

When rates are expressed in terms of unit leaf area (Fig. 6) blackjack oak seedlings surpass northern red oak seedlings at all light intensities. This can be explained by the fact that the seedlings of

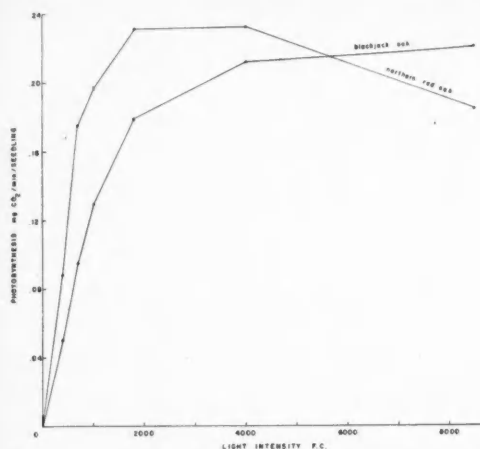


FIG. 5. The effect of light intensity on apparent photosynthesis of northern red and blackjack oak seedlings. Rates in mg CO_2 uptake per minute per seedling.

the first species had from 5 to 7 leaves, inserted on the stem at about the same level, which did not shade each other. On the contrary, the 7 to 10 leaves of the northern red oak seedlings were larger and grouped in two distinct false whorls so that the lower leaves were considerably shaded.

The differences between the responses of the two species with regard to light intensity may account for the elimination of blackjack oak by competition in sites where soil moisture conditions are favorable and which support the dense canopy of white oak-black oak-red oak forest.

EFFECT OF SOIL MOISTURE ON APPARENT PHOTOSYNTHESIS OF NORTHERN RED AND BLACKJACK OAK

This experiment was designed to test whether blackjack oak seedlings, already known to be more drought resistant than northern red oak seedlings, would prove also to be able to carry on photosynthesis more efficiently as soil moisture decreases from field capacity to wilting percentage.

METHOD

The soil moisture being brought to field capacity, the clay pots were placed in watertight metal containers and covered with two layers of oil cloth tightly fitted. Watering was then discontinued. It could thus be assumed that subsequent loss of water would be due to transpiration of the seedlings alone. Knowing the weights of dry soil, pot, oil cloth, and seedling, it was possible to determine soil moisture content from the total weight at any time.

Photosynthesis was measured at regular intervals as the soil dried until the rates became practically nil.

Six seedlings of each species were used. In each run they always came in the same order, a blackjack oak seedling alternating with a northern red oak seedling. In this manner each plant was always

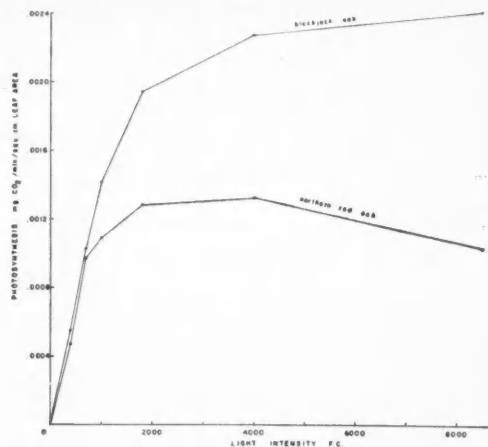


FIG. 6. The effect of light intensity on apparent photosynthesis of northern red and blackjack oak seedlings. Rates in mg CO_2 uptake per minute per sq cm of leaf area.

run at about the same time of day. Since rates were expressed in percent of the observed maximum for each seedling, the possible effect of time of day on photosynthesis was eliminated.

All measurements were made at a light intensity of 4000 f.c., an intensity previously shown to effect rates at or near the maximum for both species. Under a constant light intensity, temperature control was effective.

RESULTS

For a comparison between species, the data were submitted to regression analysis. A semi-logarithmic transformation was found to yield a rectilinear type of relationship between photosynthetic rate and soil moisture. The regression equation was of the form: $Y = b_0 + b_1 x_1$ where Y is the rate in percent of observed maximum and x_1 the logarithm of the percentage of soil moisture. Numerical values were calculated for the coefficients. The final equations were: for northern red oak seedlings, $Y = -150.6058 + 159.5870 x_1$; for blackjack oak seedlings, $Y = -123.6991 + 143.2626 x_1$.

These equations are presented in graphic form in Figure 7. The rates of blackjack seedlings seemed to decrease less than those of northern red oak seedlings at low soil moisture contents. To test if such differences were of any significance, the respective coefficients of the two regression equations were tested against each other by comparing the mean square of residuals of a general and of a common regression equation against those of the individual regressions (Table 21). The differences were not significant. In plotting the points for each individual seedling, a marked discrepancy appeared between one of the blackjack oak seedlings and the five others at low soil moisture contents. The regression equation calculated from the data of the latter five seedlings was: $Y = -122.1075 + 145.0990 x_1$. When

compared with the equation for the northern red oak seedlings, the b_1 coefficients were not significantly different but the b_0 coefficients were different (at the 1% level). It is possible that some systematic error affected the data obtained from the sixth seedling. Even if such was the situation, the differences between the five other blackjack oak seedlings and the six northern red oak seedlings, although significant, would still be small. They would undoubtedly correspond to differences in rates of growth at low soil moisture that would be too small to influence the distribution of both species in the field. At best, they would indicate that the more drought resistant species, blackjack oak, is able to carry on apparent photosynthesis at a lower soil moisture content than northern red oak.

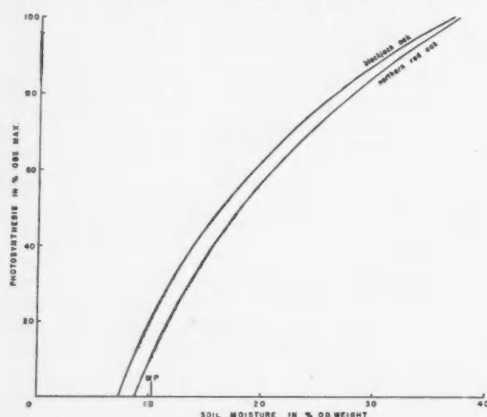


FIG. 7. The effect of soil moisture on apparent photosynthesis of northern red and blackjack oak seedlings. Rates in % of observed maximum.

TABLE 21. Regressions of apparent photosynthetic rates in % of observed maximum on log, soil moisture content.

NORTHERN RED OAK				
Source of variation	Sums of squares	Degrees of freedom	Mean square	F ratio
Regression on x_1	4449085.9	1	4449085.9	138.520
Residuals	1734411.1	54	32118.7	Highly sign.
Total	6183497.0	55		
BLACKJACK OAK				
Regression on x_1	4496315.2	1	4496315.2	161.393
Residuals	1504408.7	54	27859.4	Highly sign.
Total	6000723.9	55		
NORTHERN RED VERSUS BLACKJACK OAK				
Differences in adjusted means	85540.3	1	85540.3	2.852
Differences in regressions	25898.8	1	25898.8	Not sign.
Residuals around individual regressions	3238819.8	108	29989.1	.863
Residuals around general regression	3350258.9	110		Not sign.

GENERAL DISCUSSION AND CONCLUSIONS

The chief variations of upland oak-hickory forest in the North Carolina Piedmont are easily recognizable because of the differing oak components. Each of these communities is quite obviously associated with site quality, which may be distinguished as good, intermediate, and poor. Northern red, scarlet, black, and white oak are segregated on the best sites, from which post, blackjack, and to some extent, southern red oak are practically excluded.

There have been presented in detail the results of experimental studies designed to determine the causes for the segregation of these oak species. The implications of these results, as they are interrelated and in terms of the general environment, need now to be evaluated. Two pertinent and major considerations immediately present themselves: 1) the environmental differences between the good and poor sites and 2) the physiological differences among the segregated species.

ENVIRONMENTAL DIFFERENCES CLIMATE AND MICROCLIMATE

General climate has, of course, no bearing in the local occurrence of the various types of oak-hickory forest but it is mentioned here because it seems to be the determining factor in segregation at the western limit of the oak-hickory forest (Texas and Oklahoma). There, the post oak-blackjack oak type is reported to form the westernmost outposts of deciduous forest, transitional to the prairie (Braun 1950). Under the dry climate prevailing in these areas this type is apparently the true climatic climax.

Some microclimatic factors may contribute substantially to the local segregation of types. For example, a southern exposure, usually with rocky soil, may effect the same vegetational response as that of Orange soil on level ground: a post oak-blackjack oak forest.

Microclimate very near the ground may be selective because of its effects on seeds and seedlings. Light and temperature differences on the forest floor are greatly influenced by the density of the stand. The relatively open canopy of post oak-blackjack oak stands allows far more light and heat to reach the forest floor than in the denser white oak-black oak-red oak stands. The field plots established in the two types received 40% and 10% of the full sunlight, respectively. Of course, shade tolerant species will be increasingly favored as light is reduced. A second effect of a dense canopy is the production of more litter, which offers better protection to dormant or germinating seeds against extremes of temperature and moisture. Such a protection might be favorable to certain species and will be further discussed when the physiological differences among species are considered.

SOIL-PHYSICAL PROPERTIES

The Orange, Iredell, and other so-called "blackjack" soils are characterized by a very compact,

impervious, clayey B horizon, which is extremely hard when dry and very plastic when wet. Georgeville soils, on the other hand, have a very friable clayey subsoil. Water percolates readily through them because of the good friable structure of the clay and run-off is small. Percolation rates per minute were found to be 198 ± 16.8 cc in Georgeville and only 8.2 ± 1.3 cc in Orange soil (Korstian & Coile—unpublished data, after Duncan 1941). Percentages porosity (sum of % air and water-holding capacities) were about equal at the 2-4 in. depth in both soil series, but at the 10-12 in. depth, the Orange soil was considerably less porous (28.57 versus 44.87 for Georgeville) (Duncan 1941).

As a result of the differences in texture and structure of the horizons, less available water is retained in the surface soil, during drought periods, on Orange than on Georgeville sites.

After heavy rains, on the contrary, slow percolation through the Orange profile results in waterlogging and poor aeration of the soil, especially on level ground. In the Piedmont this usually happens in winter and early spring but during years with high precipitation soil waterlogging may persist throughout the beginning of the growing season.

Because of its compactness, the Orange B horizon must also be a greater obstacle to root penetration than the corresponding horizon in Georgeville soil.

The physical properties of the two soils are thus quite different. Those of the Orange soil are less favorable to plant growth in general. How this may affect species composition of the forest types will be assessed in the discussion of physiological differences among species.

SOIL-CHEMICAL PROPERTIES

The Georgeville and Orange series are reported as belonging to the same soil family, the Georgeville soil family, derived from fine-grained acidic rocks of metamorphic and igneous origin which are a part of the Carolina Slate complex (Lee 1947). Actually, basic rocks, together with acid ones are involved in the formation of the Orange soils (T. S. Coile. Personal Communication). Consequently more exchangeable bases and generally speaking a higher fertility are to be found in the latter soil series. The most common "blackjack soils" of the Piedmont belong to the Iredell series, derived from basic igneous rocks, and having one of the highest fertility levels of the local soil types. Plants potted in Iredell surface soil will make very good growth, yet, in the field, Iredell sites are extremely poor. By and large, the importance of soil fertility is greatly overshadowed by that of the physical properties. This point was established by Coile's work (1948) on site-index for loblolly and shortleaf pine in the Piedmont. For all the soils of this region, including Georgeville and Orange, the site-index was found to be significantly correlated only to two physical properties of the soil: the thickness of the A horizon and the imbibitional water value of the B horizon. Coile's equations, based only on these two physical charac-

teristics, estimate the site-index of all local soils with an error of about 11%. This means that about 89% of the productivity of a site is determined by them. The remaining 11% include fertility and all other environmental factors plus the sampling error. Thus by using the site-index for loblolly pine (total height of the dominant trees in a stand) as a criterion of the productivity of the soils underlying the fieldplots described earlier, those of the Georgeville series have an average site-index of 81, those of the Orange series an average site-index of only 58. Now, in hardwood forest, the differences in productivity, expressed previously in terms of growth of pine, become qualitative as well as quantitative: post and blackjack oak replace white, black, scarlet, and northern red oak and their growth is poor, the resulting stand being quite open and of small height (30 ft.).

Differences in fertility levels are thus not pertinent to the problem of oak segregation since the poorer sites are precisely those with the higher fertility.

Determinations of pH of the A and B horizons of the field-plot soils showed the same small range of variability for each soil series (4.05 to 5.70). Similarly differences in total amount of nitrogen between the two soil series (Korstian & Coile 1938) were too small to be of any importance.

No hypothetical chemical factor inhibiting completely the growth of some oak species is present in either soil series since seeds of all the species involved germinated and developed into seedlings when planted in both soils. This was also observed by Duncan (1941) in his study of root development in Orange, Georgeville, and Congaree soils.

BIOTIC FACTORS

Competition. When plants are in competition for light, moisture, and nutrients, the individual which has the greatest growth rate surpasses the others in shoot height and extent of root system. It soon overtops its smaller neighbors and these will eventually die if they are intolerant to shade. It will also deprive them from their water supply because of the greater absorbing surface of its root system. Under a dense canopy, shade tolerant seedlings will grow faster than non-tolerant ones and eventually eliminate them.

White oak-black oak-red oak stands have a much denser canopy than post oak-blackjack oak stands. If all other conditions were equal, shade tolerant species would be favored in the first stands.

Root competition is more difficult to assess. Korstian & Coile (1938) showed that the concentrations of roots of all sizes were greater at all depths in white oak-black oak-red oak stands than in post oak-blackjack oak stands. Yet it does not necessarily follow that root competition is greater in the first stands. In uneven-aged forests it can be assumed that the soil carries the maximum amount of vegetation compatible with the productivity of the site. The soil is root saturated. Consequently, root

competition should be equal in any such stand although root concentration may vary widely.

Availability of seeds. Availability of seeds is a biotic factor which is important in the initiation of secondary succession. Where climax vegetation is concerned, however, it can be assumed that, through the course of time, seeds of all species of a region have reached all stations at one time or another and have had a chance to become established anywhere. In the present problem, especially, the factor of seed sources has no importance since the various oak-hickory association-segregates may grow contiguously on either side of a sharp soil type boundary. Yet, there is no evidence of successful invasion of one forest type by the other.

Destruction of seeds by animals is an important factor in oaks. Korstian (1927) estimates that 90 to 100% of the acorn crop may be consumed or otherwise destroyed by animals. Acorns from the white oaks (subgenus *Leucobalanus*) seem to be more susceptible to destruction of this kind than acorns of the red oaks (subgenus *Erythrobalanus*), presumably because of their thinner and softer pericarp and sweeter taste. For instance, Korstian found that destruction by rodents amounted to 74.78% of the acorn crop of chestnut oak, 72.20% of that of white oak, and only 56.57% of that of red oak. On the contrary acorns of the red oaks were more subject to destruction by insect larvae than acorns of the white oaks (24.19% versus 10.57%). The seed destruction factor is of no importance in this problem since the differences in susceptibility of the various species correspond to the taxonomic groups, not to the ecologic affinities. Furthermore there is no reason to believe that rodents or insects would be more active in white oak-black oak-red oak stands than in post oak-blackjack oak stands, or vice-versa.

Plant Antagonism. The inhibiting action of some element of the soil microflora on the germination and growth of some of the oak species, or a similar antagonism between some oak species do not exist since: 1) seedlings of all species tested developed from acorns planted in both good and poor sites, in the present investigation as well as in Duncan's work (1941); 2) representatives of all species thrived when grown together in close association in the same pot.

Summing up this review of environmental factors, it appears that a number of them can be discarded by *a priori* reasoning. Those which seem to produce real differences between good and poor sites are: the microclimate of the ground level as it affects overwintering seeds, the physical properties of the soil (water relations, aeration, mechanical resistance to root penetration), light and plant competition.

PHYSIOLOGICAL DIFFERENCES AMONG SPECIES

The responses of the various oak species to the preceding environmental factors were investigated in field and greenhouse experiments.

RESPONSES TO OVERWINTERING CONDITIONS

The scant litter of post oak-blackjack oak stands offers less protection to overwintering acorns against low temperatures and desiccation than the thick litter of white oak-black oak-red oak stands. Acorn viability may be expected to be reduced under these unfavorable conditions. To affect species segregation by site, however, this reduction in viability should be differential among species and agree with their ecological affinities. Destruction of acorns by animals during the course of the experiment prevented adequate data to be obtained for the various species except northern red oak. Acorns of the latter species, after overwintering in a post oak-blackjack oak stand, had their viability reduced to about half that of those overwintering in a white oak stand. The meaning of this difference is hard to evaluate since no comparisons among species were possible.

Korstian (1927) found a marked decrease in viability of white oak acorns when their moisture content was reduced to less than 50% of their dry weight; in northern red oak acorns, on the other hand, a similar reduction in viability occurred only when their water content fell below 30%. This difference was attributed to the higher oil content of the red oak acorns. Although the pericarp of acorns of the latter species is thicker than that of white oak acorns, the rate of water loss was similar in both species. Susceptibility to injury from low temperatures was also investigated by the same author. Acorns of the white oak group were found more susceptible because of their earlier germination. Thus the differences among species was related to their taxonomic grouping and are meaningless in the present ecological problem.

RESPONSE TO DROUGHT

The field plot experiment was designed to test the effect of the environmental complex as a whole on seedling establishment and growth of the different species. Seedlings of all species developed from acorns planted in both situations and initially northern red, scarlet, and white oak were as successful, if not more so, than post and blackjack oak on the Orange sites. As the growing season went on, however, more and more seedlings of the species of the first group died on Orange soil while they survived in great numbers on Georgeville soil. There was also a difference in the appearance of the seedlings. On the poor sites they had a paler foliage which died earlier in the fall than on the good sites. Dying seedlings presented drought symptoms. The differences in survival between good and poor sites for these species were statistically significant. Simultaneously, there was significantly less available water in the poor than in the good sites. There was also more light reaching the forest floor in the poor sites, and consequently higher temperatures of seedlings and soil and more evaporation of water from the

soil. Thus, light indirectly enhanced the moisture stress of the plants.

Seedlings of post and blackjack oak, on the other hand, survived as well and had an equally healthy appearance on both sites.

The preceding evidence indicates that soil drought might be the responsible factor for the mortality of some species on Orange soil and differential drought resistance among species the cause of differential survival. An experiment conducted under controlled conditions proved the latter point. Post and blackjack oak seedlings withstood drought better than white, northern red, and scarlet oak seedlings did, under strictly identical conditions. In attempting to detect the cause of greater drought resistance, it was found that post and blackjack oak seedlings are no more able than those of the other species to resist dehydration under moisture stress. Their root extent is not greater and transpiration is not lower at low soil moisture content or under high evaporation stress than in the other species. The real cause of greater drought resistance seems rather to reside in an ability to withstand a greater degree of desiccation of the leaf tissues and yet still recover turgidity when the water supply is restored.

The clean-cut differences in survival among species on the field plots were accentuated by the subnormal precipitation during the summer of 1953. If spring and summer precipitation had been above normal, differences in survival may not have appeared among the one-year-old seedlings grown on Orange soil. This might explain why Duncan (1941) obtained such high survival percentages for various species of oaks and other genera on Orange as well as on Georgeville soil. During the year his experiment was conducted 20.25 in. of rain fell between May 1 and August 15 (normal precipitation 15.50 in). Available water in Orange soil was accordingly higher, at all times, than in 1953, when the precipitation for the corresponding period amounted to only 6.95 in. Consequently it might be possible for northern red, scarlet, and white oak seedlings to survive in post oak-blackjack oak stands for one or more growing seasons but they would eventually be eliminated during the first following dry summer.

RESPONSE TO SOIL WATERLOGGING

Seedlings of all species successfully withstood continuous soil flooding for periods of time much prolonged beyond what they might encounter in the field on any upland area. A certain proportion of seedlings of each species died but no marked differences appeared among species. In all species adventitious roots developed that replaced the original ones in the function of water absorption.

RESPONSE TO MECHANICAL RESISTANCE TO ROOT PENETRATION

Roots of seedlings of all species penetrated freely into the friable clay of the Georgeville B horizon but seemed to be hindered by the compact clay of

the Orange subsoil. Data on older seedlings with deeper root systems would be needed to establish whether there are differences among species in the ability to penetrate into compact soil layers. It is unlikely, though, that any striking difference would appear, considering Duncan's (1941) data on two-year-old seedlings.

RESPONSE TO LIGHT AND PLANT COMPETITION

Determinations of apparent photosynthesis showed that northern red oak seedlings are quite efficient in accumulating dry matter at low light intensities since their peak of photosynthetic activity was reached at about 1800 f.e. At 690 and 1000 f.e. photosynthesis amounted to, respectively, 75% and 90% of the observed maximum. Above 4000 f.e. and under higher temperatures such as the ones to which the seedlings might be subjected in the field, their apparent photosynthetic rates decreased. Blackjack oak seedlings, on the contrary, attained their maximum rate at the highest light intensity tested and were rather inefficient under low light (about 42% and 56% of observed maximum at 690 and 1000 f.e., respectively). By comparing absolute rates of photosynthesis per seedling it appears that even-aged representatives of both species carried on photosynthesis at the same rate at a point between 4000 and 8500 f.e. (Figure 5). Under lower light intensities northern red oak seedlings are more and more efficient than blackjack oak seedlings as light decreases. Data obtained from the field plots confirm this point. Over all plots, seedlings of the various species ranked as follows in the order of decreasing amount of growth: northern red, scarlet, white, blackjack, and post oak. Additional supporting evidence was obtained from potted seedlings grown in favorable water conditions under the dense canopy of a large post oak. The average total dry weights and heights at the end of one growing season, based on 12 replications, are given in Table 22.

TABLE 22. Growth of seedlings at field capacity under shade.

Average total dry weights, shoot heights, and levels of significance of their differences.

Average dry weights gm.	Species	Scarlet oak	White oak	Blackjack oak	Southern red oak	Post oak
19.937	Northern red oak	1%	5%	1%	1%	1%
11.348	Scarlet oak	1%	1%	1%
8.856	White oak
5.710	Blackjack oak	5%
4.246	Southern red oak
2.367	Post oak

Average shoot heights cm.	Species	Scarlet oak	White oak	Blackjack oak	Post oak	Southern red oak
25.7	Northern red oak	1%	5%	1%	1%	1%
16.6	Scarlet oak	5%	5%	1%
15.8	White oak
12.7	Blackjack oak
10.4	Post oak
9.9	Southern red oak

The preceding data on photosynthesis and growth demonstrate that under low light intensity and favorable soil moisture conditions, as found in the forest type on good sites, northern red, scarlet, and white oak seedlings will outgrow post and blackjack oak seedlings and, in competition, eventually eliminate them. Even in post oak-blackjack oak stands species of the first group would still make better growth if they were not more susceptible to drought injury.

Determinations of apparent photosynthesis at low levels of soil moisture failed to show any outstanding superiority of the drought resistant species in the ability to accumulate dry matter under such conditions.

RESPONSE TO DESTRUCTION OF AERIAL PARTS

Oak seedlings injured by drought, flooding, or any other cause may still be able to recover through subsequent sprouting. However no differences among species were found with regard to sprouting ability. Consequently lesser drought resistance of seedlings of a given species could not be compensated for by a greater sprouting ability.

GENERAL CONCLUSIONS

The problem, as originally stated, was to explain (1) the exclusion from poor sites of the oak species normally occurring on good sites and (2) the exclusion from these same good sites of the species appearing regularly on poor sites. The results of the study strongly support insufficient drought resistance in species of good sites as an explanation of point (1) while shade intolerance and lower growth rate with resulting elimination in competition explain the exclusion of poor site species from good sites.

SUMMARY

1. This investigation was made to determine reasons for the segregation of oaks in the Piedmont upland oak-hickory forest into three types related to site quality. The white oak-red oak-black oak type is restricted to the best sites, the white oak-post oak to sites of intermediate quality, and the post oak-blackjack oak type to the poorest sites (thin, rocky soils on southern exposures; eroded areas; soils with a plastic, impervious B horizons).

2. Most of the upland oak species (white, northern red, scarlet, black, southern red, post, and blackjack oak) were used in some phase of the investigation, which was limited to the seed and seedling stages. Sites on Orange and Georgeville soil series were selected as representatives of poor and good sites, respectively.

3. Acorns of the various species were exposed over winter to the conditions prevailing under the thin litter of post oak-blackjack oak stands on Orange soil and under the thick litter of white oak-black oak-red oak stands on Georgeville soil. Except for northern red oak, which had about half the viability after storage on Orange as on Georgeville soil, the data were inconclusive. In view of the information on acorn germination found in the literature,

it is doubtful that field overwintering conditions have any importance in the segregation of species by site.

4. Acorns of good site species (northern red, scarlet, and white oak) and of poor site species (post and blackjack oak) were planted in field plots established on Orange soils in post oak-blackjack oak stands and on Georgeville soils in white oak-black oak-red oak stands. Seedling survival of good site species was considerably and significantly less on Orange than on Georgeville soils. It was also less than that of the poor site species on the same Orange soils. Simultaneously there was significantly less available water in the Orange surface soils than in the Georgeville surface soils during the very dry summer of 1953. Moreover the dying seedlings showed drought symptoms. It was concluded that the high mortality of seedlings of good site species on poor sites was due to their inability to withstand soil drought.

Generally speaking seedlings of all species still surviving at the end of the growing season did not make significantly more growth (total dry weight, shoot height and diameter, root length) on Georgeville than on Orange soils. Shoot-root ratios had a greater correlation with taxonomic than ecologic affinities of the species: seedlings of white oaks had smaller shoot-root ratios than seedlings of red oaks. Root penetration of the plastic and compact Orange subsoils seemed to be hindered for one-year-old seedlings of all species.

5. The relative drought resistance of the various oak species was tested under controlled conditions. Post and blackjack oak seedlings proved to be more drought resistant than seedlings of white, northern red, and scarlet oak.

6. In an attempt to determine the cause of differential drought resistance among oak species, transpiration of seedlings under various conditions, leaf moisture retention, and osmotic pressure of the leaf cell sap were measured. Transpiration rates were not significantly different among species with the soil at moisture contents ranging from field capacity to wilting percentage, nor under high, medium, and low evaporation stresses. Osmotic pressures of leaf cell sap were not markedly different among species. Leaf moisture retention, with the soil at the wilting percentage or below, was significantly less in the more drought resistant species, yet their leaves recovered turgidity when the water supply was restored. Moreover, seedlings of the more drought resistant species did not have a relatively greater root extent than those of the less drought resistant species. It is concluded that the cause of greater drought resistance of post and blackjack oak must reside in an ability of the leaf tissues to withstand successfully a greater degree of dehydration.

7. Tests of sprouting ability after injury to the shoots showed that seedlings of all the oak species investigated sprouted equally well.

8. Since Orange soils are waterlogged at times because of the impervious nature of the B horizon, the ability of the various species to withstand soil flooding was investigated. No differences appeared among species in transpiration rates nor in survival under these conditions. Most of the seedlings of all species survived long periods of soil flooding and all developed adventitious roots.

9. Growth response to various conditions of light and soil moisture was investigated by measurements of apparent photosynthesis. Blackjack oak seedlings were relatively inefficient at low light and their photosynthetic rates kept increasing with increasing light intensity. Seedlings of northern red oak attained their peak of photosynthetic activity at relatively low light intensity. These results established the shade intolerance of blackjack oak and the shade tolerance of northern red oak, at least in the seedling stage.

The photosynthetic rates of seedlings of both species decreased with decreasing soil moisture in about the same proportion. At low soil moisture content, blackjack oak seedlings were slightly more efficient than northern red oak seedlings, but not significantly so.

10. Consideration of the environmental conditions prevailing on Georgeville soil under white oak-black oak-red oak forest and on Orange soil under post oak-blackjack oak forest led to the conclusion that these sites differ in:

- (1) less favorable seed overwintering conditions under the litter of the post oak-blackjack oak stands.
- (2) the physical properties of the soil
 - (a) Orange soils retain less available water during dry spells
 - (b) Orange soils are exposed to winter and spring waterlogging
 - (c) Orange subsoils offer a greater resistance to root penetration
- (3) the conditions of light and plant competition: the dense canopy of the white oak-black oak-red oak stands allows less light to reach the forest floor and consequently shade tolerant species are favored.

11. In view of the demonstrated physiological differences among seedlings of the various species and considering the environmental differences just enumerated, it is concluded that (1) good site species (northern red, scarlet, white oak) are eliminated from the poor sites because of insufficient drought resistance; seedlings of these species may be able to survive on the poor sites for one or more growing seasons but they will be eliminated during the first following dry summer; (2) because of their shade intolerance and slow growth, poor site species (post and blackjack oak) are eliminated from good sites in competition with good site species under the dense canopy of white oak-black oak-red oak stands.

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